ANNALES

de la
SOCIÉTÉ SUISSE DE ZOOLOGIE
et du
MUSÉUM D'HISTOIRE NATURELLE
de la Ville de Genève

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Le comité soumet chaque manuscrit pour évaluation à des experts d'institutions suisses ou étrangères selon le sujet étudié.

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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 2

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The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 2. - This study concludes the series of reviews on European athecate hydroids and anthomedusae, providing updated classifications, descriptions, and illustrations of all species. The present work mainly treats the remaining capitate families, but taxonomic comments and updates on some filiferan taxa are also given.

The genus name *Russellia* Kramp, 1957 is preoccupied and the new name *Heterotentacula* **n. gen.** and the family level name Heterotentaculidae **n. fam.** are proposed to replace them. *Janiopsis* Bouillon, 1980 is also a preoccupied genus name. No replacement name is necessary as *Janiopsis* is regarded as congeneric with *Merga* Hartlaub, 1914. The frequently used genus name *Heterotiara* Maas, 1905 is invalid and must be replaced by *Protiaropsis* Stechow, 1919.

Tubularia ralphi Bale, 1884, *Tubularia gracilis* von Lendenfeld, 1885, *Tubularia australis* Stechow, 1924, and *Tubularia warreni* Ewer, 1953 are all recognized as new synonyms of *Ectopleura crocea* (L. Agassiz, 1862). Mediterranean records of *Ectopleura minerva* Mayer, 1900 are here attributed to *E. wrighti* and *E. minerva* does not likely occur in European waters. A reexamination of the type material of *Corymorpha appelloefi* Bonnevie, 1901 made it clear that it must be regarded as synonym of *Corymorpha nutans* M. Sars, 1835. *Meiorhopalon arenicolum* Salvin-Plawen, 1987 is recognized as a new synonym of *Euphysa aurata* Forbes, 1848. Examination of the type material of *Coryne filiformis* (Rees, 1936) showed that it is inseparable from *Coryne pintneri* Schneider, 1898. *C. filiformis* must thus be regarded as a new synonym of *C. pintneri*. *Eugotoea petalina* Margulis, 1989 is likewise a new synonym of *Rhabdoon singulare* Keferstein & Ehlers, 1861.

Keywords: Anthoathecata - Capitata - Europe - taxonomy - species - systematics - revision - review.

INTRODUCTION

This publication concludes the series of systematic reviews and revisions of the European athecate hydroids and anthomedusae (Schuchert, 2001b; 2004; 2006; 2007; 2008a; 2008b; 2009). The report treats the remaining families of the suborder Capitata, but some supplementary information relating to members of the Filifera and omitted in the previous studies is provided below.

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Hydromedusae and hydroids assigned to the suborder Capitata are distinguished by their cnidome that always includes stenotele capsules (Bouillon *et al.*, 2006). Major revisions of the group have been undertaken by Rees (1957) and Petersen (1990). Recent molecular evidence indicates that Capitata is not a clade and comprises two unrelated groups (Collins *et al.*, 2005; Daly *et al.*, 2007; Cartwright *et al.*, 2008; Nawrocki *et al.*, 2010). Likewise, the sister taxon of the Capitata, Filifera, as well as the more inclusive taxon Anthoathecata, appear also to be polyphyletic. Although the available results are not yet comprehensive enough to allow constructing a complete, robust and coherent classification, it is already clear that in near future profound changes of the hydrozoan classification will take place. For the Capitata *sensu* Bouillon *et al.* (2006), there is already enough evidence available that this taxon must be split into two groups, namely Capitata *sensu stricto* and Aplanulata (Collins *et al.*, 2005; Nawrocki *et al.*, 2010). Both will likely obtain the status of an order. However, in order to continue with the same classification system as used in the previous studies of this series, the suborder Capitata sensu Petersen (1990) is here used again. Nevertheless, the families are here separated into the two clades of the coming new system.

The taxon Filifera will likewise be abandoned and split into several groups (Cartwright *et al.*, 2008), but the currently available data are still incomplete a revised classification is premature. Some remarks relating to filiferan species treated in previous papers have become necessary.

One new filiferan family has recently been created and was not listed or treated in the previous publications, namely the Tubiclavoididae Moura, Cunha & Schuchert, 2007. The family comprises one species, *Tubiclavoides striatum* Moura, Cunha & Schuchert, 2007 occurring in deep waters of the Gulf of Cadiz.

Dr Theo Engeser (Berlin) kindly brought to my attention that some names used in previous publications of this series are actually invalid homonyms and need to be replaced.

Heterotiara Maas, 1905 is an invalid homonym of *Heterotiara* Pomel, 1883 [Echinodermata, fossil]. This has already been recognized by Stechow (1919: 150) who proposed the replacement name *Protiaropsis* Stechow, 1919. The only species of this genus, treated in Schuchert (2009), must thus correctly be named *Protiaropsis anonyma* (Maas, 1905).

Russellia Kramp, 1957 is preoccupied by *Russellia* Vargas, 1943 [Insecta, Diptera] and *Russellia* Muesebeck, 1950 [Hymenoptera]. The family name Russellidae Kramp, 1957 thus also becomes invalid (see Schuchert, 2009). As a replacement names I propose the genus name *Heterotentacula* **n. gen.** and the family level name Heterotentaculidae **n. fam.** The type species for *Heterotentacula* is *Russellia mirabilis* Kramp, 1957, to be used in the combination *Heterotentacula mirabilis* (Kramp, 1957) **n. comb.** The name *Heterotentacula* is an allusion to the two different tentacle types that characterize the medusa.

Janiopsis Bouillon, 1980 is preoccupied by *Janiopsis* Rovereto, 1899 [Gastropoda, Buccinidae; fossils]. In my opinion, *Janiopsis* Bouillon, 1980 is congeneric with *Merga* Hartlaub, 1914 and there is thus no need to introduce a replacement name. *Janiopsis* Bouillon comprised only one species, which must be used in the combination *Merga costata* (Bouillon, 1980) **n. comb.** if *Janiopsis* and *Merga* are regarded as

synonyms. The diagnosis as given in Schuchert (2007) already fits the new scope of the genus *Merga*.

MATERIAL AND METHODS

See also the previous papers in this series (Schuchert 2001b through 2009). For a general introduction to the Hydrozoa see Bouillon *et al.* (2004, 2006).

The arrangement of the families and species follows no phylogenetic order; it merely reflects a grouping according to superficial similarity, allowing an easier comparison. Normally, the taxa are presented in the same order as they sort in the identification keys.

Where possible, species descriptions were supplemented by sequence information from part of the 16S mitochondrial rRNA gene (COI of hydrozoans is often not easily amplifiable using standard primers; unpublished observations). DNA sequence data used for taxonomic barcoding approaches (e. g. Hebert *et al.*, 2003; Packer *et al.*, 2009) can be a very useful tool for identifying species, provided a large enough database of sequences obtained from reliably identified and described specimens is available. The methods to obtain DNA sequences are described in Schuchert (2005a, 2007). All sequences have been submitted to the EMBL database (accession numbers FN687530-FN687562, FN687910). Some additional sequences available from the EMBL/GEnBank database were also used for comparisons. Their accession numbers are given in the figures (1, 73). For sequence comparisons and phylogenetic analyses, the sequences were aligned using ClustaW (Larkin *et al.*, 2007) using default parameters and then trimmed to shortest sequence. To assess the intra- and interspecific genetic variability within the genus *Zanclea*, a pairwise distance matrix with simple % sequence differences was used. The genetic diversity of species of the Tubulariidae and Corymorphidae, viz. the suitability for using 16S data for species identifications, was assessed by a phylogram resulting from a Maximum Likelhood analysis using the software PhyML (Guindon & Gascuel, 2003). The HKY model was used as base substitution model, base frequencies, transition/transversion ratio, substitution rates, and the proportion of invariant sites were estimated by the application PhyML. Other substitution models, e. g. GTR, resulted in trees that were topologically almost identical (not shown).

Abbreviations

BELUM	Ulster Museum, Belfast, Northern Ireland
BMNH	The Natural History Museum, London, England
ERMS	European Register of Marine Species (Costello *et al.*, 2001)
GNM	Gothenburg Natural History Museum, Sweden
MNHN	Musée National d'Histoire Naturelle, Paris, France
NHMW	Naturhistorisches Museum Wien, Austria
r	ratio of nematocyst length and width
ZMUB	Zoological Museum, University of Bergen, Norway
ZMUC	Zoological Museum Copenhagen, Denmark
ZSM	Zoologische Staatssammlung München, Germany

TAXONOMIC PART

Clade Aplanulata

Family Tubulariidae Fleming, 1828

Tubulariadae Fleming, 1828. [corrected to Tubulariidae by Hincks, 1868]
Tubularidae Allman, 1872. [incorrect spelling]
Hybocodonidae Allman, 1872.
Hybdocoridae Pennington, 1885. [incorrect spelling]
Hypocodonidae Grönberg, 1898: 73. [incorrect spelling]

Diagnosis: Hydroid solitary or colonial; composed of terminal hydranth on hydrocaulus. Caulus divided into upper neck region covered by filmy perisarc and lower stem covered by thicker perisarc, lower part of stem either short and thick with terminal tuber-like processes, or long and cylindrical, or cone-shaped with basal disc, or ending in stolons. Hydranth broadly vasiform, tentacles in two sets, oral ones filiform or pseudofiliform in one to several close-set whorls, sometimes capitate or moniliform (especially transiently in juveniles); aboral tentacles long, in one whorl, pseudofiliform or filiform, sitting on a more or less developed parenchymatic cushion of gastrodermal tissue; gonophores develop above aboral tentacles, free medusae or fixed sporosacs; embryonic development without planula, resulting directly in a hydranth-like actinula.

Medusae with or without exumbrellar nematocyst tracks, bell margin oblique or straight, four radial canals; mouth usually circular; gonads covering manubrium entirely; one to four marginal tentacles; with or without asexual medusae budding from marginal bulbs; ocelli absent.

Remarks: For the taxonomic history of this family see Calder (1988); for its genera see Petersen (1990) or Bouillon *et al.* (2006). New genera have been proposed by Marques & Migotto (2001) and Watson (2008), but the current system is not satisfactory and the generic separation appears artificial and overly split.

The Tubulariidae and Corymorphidae share many features and have often been united in one family (e. g. Russell, 1953; Kramp, 1961). Most modern authors followed Kramp (1949) in keeping them separate, but the limits are still not entirely resolved (Kramp, 1949, 1961; Rees, 1957; Brinckmann-Voss, 1970; Millard, 1975; Calder, 1988; Petersen, 1990; Bouillon *et al.*, 2006).

Sequence data: Partial 16S DNA sequences were obtained for a number of specimens of Tubulariidae and Corymorphidae examined for this study. The 16S sequence evolves rather rapidly and it is therefore mostly not suitable for revealing phylogenetic relationships above the species or genus level. The primary goal therefore was to see if they could be useful for species identification, e. g. for damaged specimens or juvenile individuals which lack diagnostic features. Most species are represented by only a few samples, and the study must thus be seen as a pilot experiment for a more in-depth population genetic analysis. No extensive sequence comparisons were therefore made. Instead, the sequence diversity was assessed graphically through a phylogenetic tree (Fig. 1). Intraspecific and interspecific sequence divergences can be roughly evaluated by comparing the sums of the horizontal branch lengths within a species and between species (Fig. 1: grey boxes = within species). For a good molecular barcode sequence, pairwise intraspecific differences must be significantly lower

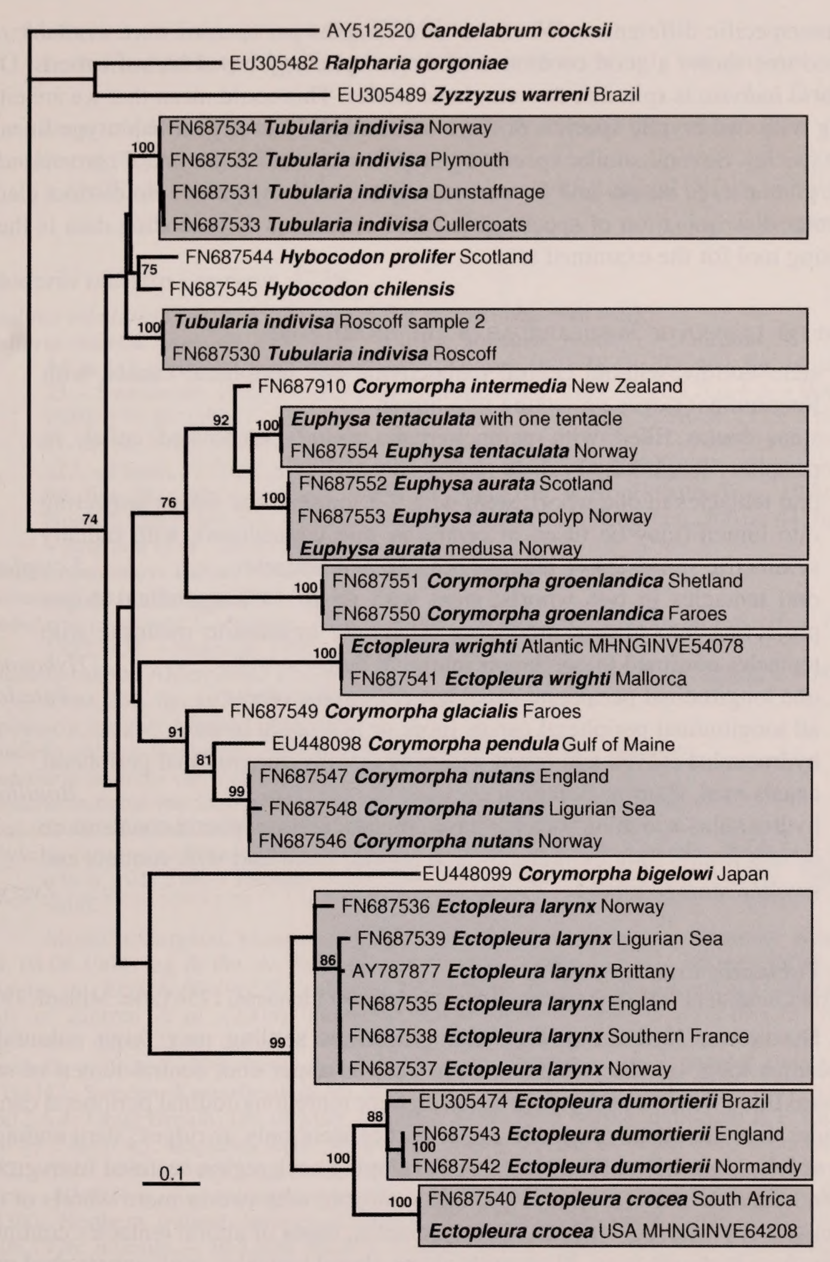


FIG. 1

Phylogenetic tree as graphic representation of 16S DNA sequences divergences of samples of Tubulariidae and Corymorphiidae examined in this study (490 bp sequence, maximum likelihood tree with % bootstrap support for each node, only values >70% given HKY model, see section Material and methods). The names of the terminal taxa are composed of the sequence accession number (some duplicate sequences lack this number), the name, and an indication of the locality or voucher number. Clades comprising identical species are framed. For more details see text.

than interspecific differences. Where several samples per species were available, the obtained tree shows a good coherence of the morphology-based identifications. Only *Tubularia indivisa* is split into two unrelated clades. This could mean that we are either dealing with two cryptic species, or there coexist highly divergent haplotype lineages in this species. Several similar species pairs (*E. crocea* and *E. larynx*, *C. groenlandica* and *C. glacialis*, *E. aurata* and *E. tentaculata*) are well-separated into distinct clades. Molecular discrimination of species using 16S sequences as barcoding data is thus a promising tool for the examined taxa.

KEY TO THE GENERA OF TUBULARIIDAE OF THE ERMS ZONE

1a	stem hollow, without central parenchyme and peripheral canals, with longitudinal ridges projecting into lumen	2
1b	stem centre filled with parenchymatic tissue (vacuolated cells), in periphery longitudinal canals	3
2a	oral tentacles in one whorl; stem with 2-5 longitudinal ridges projecting into lumen (may be fused in centre by thin connection); with radially symmetric sporosacs or medusa bearing 2- 4 tentacles	*Ectopleura*
2b	oral tentacles in two whorls; stem with up to 14 longitudinal ridges projecting into lumen; producing bilaterally symmetric medusae with tentacles confined to one larger marginal bulb	*Hybocodon*
3a	one longitudinal peripheral canal larger than the others	*Tubularia*
3b	all longitudinal peripheral canals more or less equal in size	4
4a	hydrocaulus curved and much widening distally, longitudinal peripheral canals oval, short neck region	*Bouillonia*
4b	hydrocaulus widening towards base, longitudinal peripheral canals more or less round, long cylindrical neck region, basal end with rootlets and swollen storage tubers	*Zyzzyzus*

Genus ***Tubularia*** Linnaeus, 1758

Tubularia Linnaeus, 1758; type species *Tubularia indivisa* Linnaeus, 1758 (after Millard, 1975).

DIAGNOSIS: Hydroid solitary, but gregarious settling may feign coloniality. Hydrocaulus long, tubular, widening from base to upper end, central lumen of stem coenosarc filled with parenchymatic cells, eight or more longitudinal peripheral canals, one wider than the others, canals in upper part of stem only as ridges; stem ending in stolon or lobed basal disc. Filmy perisarc enveloping neck region secreted from groove between hydranth base and neck. Hydranth vasiform, with two or more whorls of oral filiform and one whorl of filiform aboral tentacles; bases of aboral tentacles continued as ridges over hydranth base. Blastostyle above aboral tentacles, with unbranched main trunk, with or without thin side branches; gonophores reduced to sessile sporosacs, sometimes with radial canals and ring canal, with or without distal processes; radial canals when present of unequal length, circular canal and opening displaced to one side, thus rendering gonophore bilaterally symmetric.

KEY TO SPECIES OF *TUBULARIA* OF THE ERMS ZONE:

1a boreal to Arctic species, female sporosacs with no or only one process .... *T. indivisa*

1b large, cold water species, female sporosacs with more than one process 2

2a female sporosacs with 3-7 meridional crests .... *T. regalis*

2b individuals hermaphroditic, female sporosacs with 3 lateral bumps in lower half .... *T. asymmetrica*

Tubularia indivisa **Linnaeus, 1758** Fig. 2

Corallina tubularia Ellis, 1755: 31, pl. 16 Fig. c. [non-binomial work]

Tubularia indivisa Linnaeus, 1758: 803. – Ellis & Solander, 1786: 31. – Johnston, 1847: 48, pl. 3 figs 1-2. – Hincks, 1868: 115, pl. 20. – Allman, 1871-1872: 205, 400, fig. 44, pl. 20 & 23. – Swenander, 1904: 10, pl. figs 6-7. – Jäderholm, 1909: 42 pl. 2 figs 4-5. – Borowski, 1910: 230, pl. 19 fig1, 4. – Broch, 1911: 12, fig. 9, pl.1 fig 1. – Broch, 1915: 8 pl. 2 figs 11-15, pl. 3 figs 13-15. – Broch, 1916: 24, fig. D, pl. 1 fig. 4. – Weill, 1934: 366, fig. 212. – Fraser, 1937: 52, pl. 10 fig. 43. – Fraser, 1944: 98, pl. 17 fig. 91. – Vervoort, 1946: 99, figs 391, 40. – Naumov, 1969: 237, fig. 108. – Brinckmann-Voss, 1970: 32. – Hughes, 1983: 468, fig. 1A-B. – Petersen, 1990: 196. – Schuchert, 2001a: 44, fig. 31A. – Bouillon *et al.*, 2004: 109, fig. 57C-F.

Tubularia calamaris Pallas, 1766: 81. – Allman, 1872: 403, synonym.

? *Tubularia divisa* Osborn, 1893: 96.

? *Tubularia couthouyi* L. Agassiz, 1862: 266, pl. 23a figs 8-9, pl 24, pl 26 figs 1-6. – Allman, 1872: 403. – Petersen, 1990: 196, synonym.

Tubularia simplex Alder, 1862: 232, pl. 8 figs 3-4. – Hincks, 1868: 121, pl. 22 fig. 1. – Naumov, 1969: 237, fig. 107. – Petersen, 1990: 196, synonym.

? *Tubularia insignis* Allman, 1872: 405.

Tubularia obliqua Bonnevie, 1898: 474. – Swenander, 1904: 10, synonym.

? *Tubularia indivisa* var. *antarctica* Hartlaub, 1905: 537, fig. R.

Tubularia indivisa var. *littoralis* Borowski, 1910: 230, figs 1-2, pl. 19 fig. 2.

Tubularia indivisa var. *solitaria* Borowski, 1910: 230, pl. 19 fig. 3.

Tubularia ceratogyne Pérez, 1920: 27, figs 1-4. – Pérez, 1925: 185. – Weill, 1934: 363, figs 16, 43a-b, 101, 210. – Hughes, 1983: 476, synonym of *T. indivisa*. – Petersen, 1990: 197, valid.

MUSEUM MATERIAL EXAMINED: MHNG INVE 34774; North Sea, Germany, Norderney, coll. 04.06.1904; leg & det. A. Fenchel; several short stems, fertile. – MHNG INVE 54661; Belgium, 51.3955°N 02.4965°E; collected 03.05.2005; 30 m depth, on wreck; material from study of Zintzen *et al.* (2008); numerous fertile stems. – BMNH 1962.10.7.48; Norway, Rognesund; depth 25 m; collected 09.04.1962; fertile. – BMNH 1941.3.20.449; Great Britain, Plymouth; collected 1898; fertile females; collection E. T. Browne. – BMNH 1965.1.14.104 +105+112; Sweden, Kosterfjord; depth 80-120 m; collected 28.09.1964; stems only. – BMNH 1960.2.6.4; Great Britain, Isle of Man; collected 14.04.1894; fertile; collection E.T. Browne. – BMNH 1964.6.4.1; England, Kent, Whitstable Spring, the Street; depth 0 m; collected spring 1962; fertile female; very long stems (15 cm) and large hydranth, female sporosacs without crests. – BMNH, no registration number; Belgium, Ostende; several fertile hydroids. – BELUM Md300; Northern Ireland, Strangford Lough, S of Carrstown Point; depth 27 m; collected 26.06.1976; infertile. – BELUM Md454; Ireland, Saltee Islands, Wexford, Coningbeg Rock; depth 30 m; collected 26.05.1982. – ZMUC, no registration number; Norway, Trondheimsfjord; depth 300 m; collected 22.09.1934; fertile; det. Kramp. – ZMUC, no registration number; Canada, Nova Scotia, Digby Cove, Sandy Cove South Side; depth 0 m; collected 22.07.1970; fertile, leg. & det. K. W. Petersen. – ZMUC, no registration number; Denmark, Herthas Flak; depth 20 m; collected 18.09.1968; fertile. – ZMUC, no registration number; as *Tubularia ceratogyne*; England, Harwich; collected 1977 by R. Hughes, fertile polyps. – ZMUC, no registration number; as *Tubularia ceratogyne*; France, Roscoff; 15.05.1965; fertile; leg. Bouillon; male and female polyps.

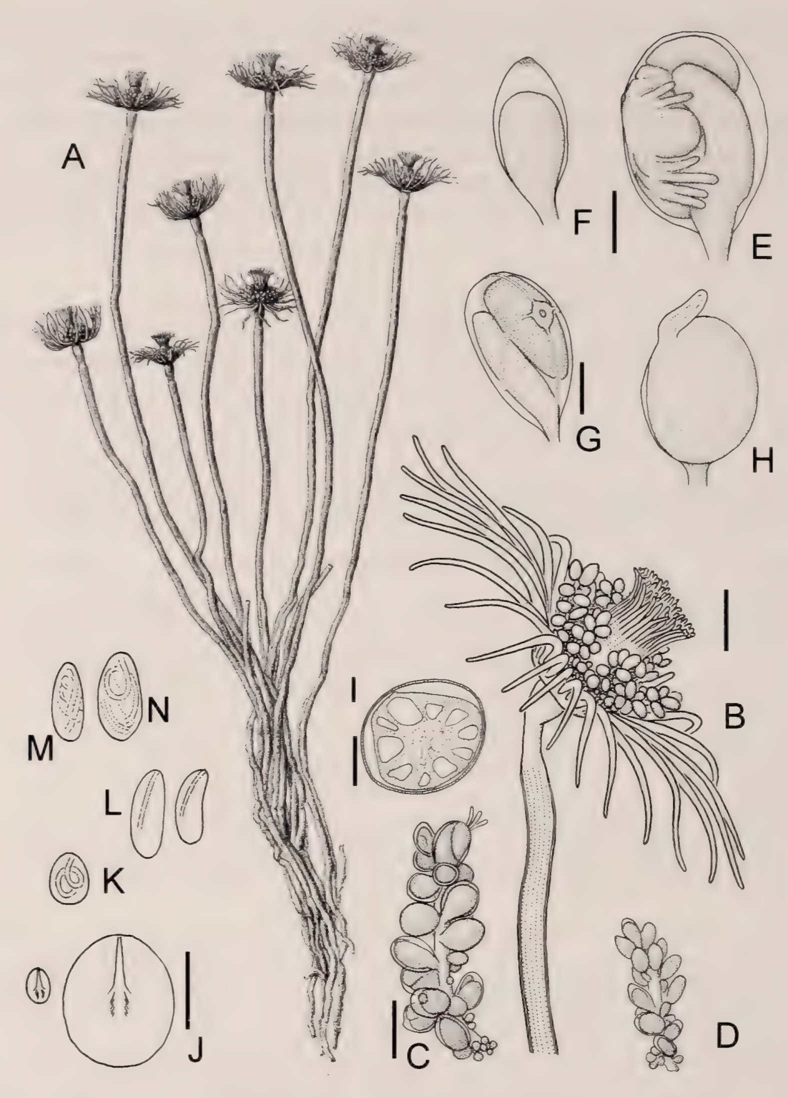


FIG. 2

Tubularia indivisa Linnaeus, 1758. (A) Part of colony, about 80% life size. (B) Hydranth with sporosacs, scale bar 2 mm. (C) Female blastostyle, after preserved material from Ostende, scale bar 0.5 mm. (D) Male blastostyle, after preserved material from Ostende, scale bar 0.5 mm. (E) Female sporosac with developing actinulae inside, radial canals are reduced, scale bar 0.5 mm. (F) Male sporosac, same scale as F. (G) Female sporosac with visible radial- and ring canal, scale bar 0.5 mm. (H) Female sporosac with tentacle-like process (*ceratogyne* form), same scale as F. (I) Schematic cross-section of stem showing peripheral canals and centre filled with parenchymatic cells, scale bar 0.5 mm. (J) Stenoteles of different size, scale bar 10 μm. (K) Desmoneme. (L) Microbasic euryteles from same polyp. (M) Anisotrichous anizorhiza. (N) Anisotrichous anizorhiza from a different population.

A, modified after Jäderholm (1909), B-F after preserved material from Ostende, G after material from Greenland, H after preserved material from Roscoff, J-M after living material from Plymouth; N after preserved material from Roscoff.

LIVING MATERIAL EXAMINED: MHNG INVE 60972; Atlantic; France, Roscoff, Trou aux singes, on stones; depth 70 m; collected 02-06.05.2008 by dredging; infertile; 16S of two colonies gave identical sequences **FN687530**. – Scotland, Firth of Lorn, Dunstaffnage Bay; depth 0 m; 03.05.2004; with developing sporosacs; no material deposited; 16S **FN687531**. – England, Plymouth; depth 25 m; collected 26.06.2007; infertile; no material deposited; two specimens gave identical 16S sequences **FN687532** – England, Cullercoats, near Dove Marine laboratory; collected March 2009; with developing sporosacs; no material deposited; 16S **FN687533**. – Norway, Raunefjord, Vatlestraumen; depth 32-42 m; 16.09.2008; with developing sporosacs; no material deposited; 16S **FN687534**.

DIAGNOSIS: Tubulariidae with perisarc originating at junction of polyp head and its neck; oral tentacles in several close-set whorls and their number at least 1.5 times higher than number of aboral tentacles, stems usually in characteristic clusters with entwined and adnate basal parts, stems 1-15 cm, hydranth diameter 3-9 mm. Female sporosac with or without one tentacle-like process, in younger stages with four radial canals of unequal length.

DESCRIPTION: Hydroid solitary (not colonial), usually growing in characteristic clusters comprising several to many individuals with twisted, entwined and often adnate basal parts of stems, stems attached to substratum by unbranched, creeping stolons. Hydroid sometimes also occurs singly.

Stem lengths of fertile hydranths very variable, depending on age and environment. Stem perisarc firm, regular annulations or nodes rare or absent, but perisarc tube in lower part often irregular and gnarled. Coenosarc of stem in centre filled with loose parenchymatic cells, 9-12 peripheral canals, one of them usually distinctly larger. The canals give the stems a longitudinal striation pattern.

Neck region with inflated, filmy perisarc originating at junction of hydranth and caulus (thus without collar on neck part), neck region about as large as hydranth.

Hydranth flask-shaped, with one aboral whorl of 20-36 fairly long aboral tentacles and 40-60 short oral tentacles in up to five closely set whorls, oral tentacles continued on hydranth body as longitudinal ridges. Proximal region of aboral tentacles laterally flattened, cross-section oval.

Gonophores borne on 8-12 long, unbranched blastostyles originating distal to aboral tentacles. Each blastostyle with up to 30 gonophores of variable size and stages, mature ones up to 10, gonophores with a short pedicel, arranged irregularly around and along the whole length of the blastostyle.

Gonophores remain fixed as sporosacs. Female sporosacs ovate to globular, with rounded distal end, spadix shifted to one side. During development usually with four radial canals of unequal length and a circular canal, circular canal opening shifted to side, thus rendering symmetry bilateral. Lateral shift of opening rather variable, the opening can thus be terminal, subterminal or lateral. Radial canals in later development canals usually absent or reduced, shortest one remains more frequently. Even when present, radial canals often difficult to see as very flat and lumen closed, especially so in preserved material. A red pigment can render canals more visible in living material.

Female sporosacs in some populations and under certain conditions developing a tentacle-like process near distal end of shortest radial canal (*ceratogyne* form), size of process and fraction of sporosacs bearing a process variable, may reach 100%. Eggs develop into actinulae in situ, 1-2 per sporosac. Actinulae resemble small polyp heads,

with long, filiform aboral tentacles at time of liberation, oral tentacles as small bumps around mouth, just beginning to develop. A few tentacles of actinula often protrude from opening of the sporosac. Actinulae settle preferably on stems of other *T. indivisa* polyps, hence philopatric.

Male sporosacs oval to globular, smaller than female ones, at no stage with radial canals or ring canal, no tentacle-like process.

Nematocysts: stenoteles of several size classes; desmonemes, discharged with three coils; microbasic euryteles, discharged shaft about 0.7 times the capsule length; heterotrichous anisorhizas.

Colours: polyp colour pale pink to red, spadices of sporosacs likewise, sometimes also radial canals red; gametes white; stem perisarc in order animals yellow.

DIMENSIONS: Stem heights usually around 5-15 cm, but heights of up to 20 cm have been reported. Stem can also be very short (1 cm) in animals from shallow waters. Diameter of hydranth body at site where aboral tentacles insert 3-9 mm (for mature polyps). Stem diameter up to 2.5 mm, more usually 0.8-1.5 mm. Aboral tentacles contractile, in preserved animals longer than hydranth diameter, living much longer. Female sporosacs 1.6 mm long, male ones 1.2 mm. Nematocysts (from several preserved animals): stenoteles (5.5-17)x(4-14)μm; desmonemes (6-7)x(4-5)μm; microbasic euryteles (9.5-13)x(4-4.5)μm; heterotrichous anisorhizas (10-14)x(4-4.6)μm r=1.9-2.6. The anisorhiza capsules show considerable variation in size and especially in the length/width ratio between individual polyps (Fig. 2M-N).

OTHER DATA: Allman (1871/72) described the morphology and the development in great detail. The development of the gonophores, especially of the radial canals and the tentacle-like process, was examined by Broch (1915). Benoît (1914) and Pérez (1913) examined the oogenesis, van de Vyver (1968) the early development, Billard (1905) the regeneration. Weill (1934) gave a detailed account of the nematocysts (for *T. indivisa* and *T. ceratogyne*).

BIOLOGY: Occurs occasionally at the low-water level in rock-pools or underneath floating pontoons, otherwise more frequently in 10 to 100 m depth, rarely also deeper. Fey (1970) studied the species in the Glenan Archipelago south of Brittany. She found it frequently at exposed sites in depths of 2-30 m, with a maximum between 3-12 m.

Tubularia indivisa is a characteristic species of current-swept bedrock and boulder bottoms, and it may also attach to other substrata such as laminarian holdfasts, wood, wrecks, etc. The stems are a substrate for a number of other hydroids and other sessile invertebrates. *Tubularia indivisa* tolerates reduced salinities down to 18 ppt (Schönborn *et al.*, 1993).

The main reproductive period in the British Isles is February to October (Allman, 1871/1872; Hamond, 1957; Russell, 1957). The animals usually overwinter as stolons, in deeper waters they may persist over the whole year (Christiansen, 1972). Fertile animals were observed from mid-December to the beginning of May.

Hughes (1983) made a detailed study of the ecology and life history of *T. indivisa*. The actinula attaches itself soon after its release, develops a hydrocaulus, and finally stolons grow from near the base. *Tubularia indivisa* is able to produce offspring

throughout the year, but recruitment is highest in spring and with a smaller peak during summer. *Tubularia indivisa* suffers greatly from predation by the nudibranch *Dendronotus frondosus*, leaving only the stems. The life span of an individual *T. indivisa* is about one year. There is no evidence that the frequently-observed autotomy of the hydranth is an integral part of the life cycle of *T. indivisa*.

Further details of its biology are given in Orlov (1996) and Zintzen *et al.* (2008).

DISTRIBUTION: A circumboreal to polar species, widely distributed in the northern parts of the Atlantic (Jäderholm, 1909; Broch, 1916; Fraser, 1944; Naumov, 1969; Christiansen, 1972; Schuchert, 2001a). Common in the British Isles, along the coasts of Norway, and the North Sea. Also present in the Baltic Sea (Schönborn *et al.*, 1993). South of Brittany its gets rarer, but it has been reported from the Atlantic coast of the Iberian Pensinsula (Medel & López-González, 1996), the southernmost records are the Azores (Cornelius, 1992), Morocco (Patriti, 1970), and Ghana (Buchanan, 1957). Also present in the North Pacific Ocean and in the Arctic Sea north of Russia (Fraser, 1937; Naumov, 1969; Petersen, 1990). Type locality: NE Atlantic (Linnaeus, 1758).

The Mediterranean records (Bouillon *et al.*, 2004) are based on Motz-Kossowska (1905) and Stechow (1923b) and need reconfirmation as they are likely wrong. Stechow (1923b) stated that the male sporosacs of his *T. indivisa* had a ring canal, which is atypical for this species.

SYNONYMY: *Tubularia calamaris* Pallas, 1766 is evidently a synonym of *T. indivisa*, an opinion already expressed by Allman (1872).

Tubularia simplex Alder, 1862 from Cullercoats (England) was based on a solitary animal. Petersen (1990) regarded it as conspecific with *T. indivisa* and I concur. Hincks (1868) and Naumov (1969) kept it distinct.

Tubularia insignis Allman, 1872 (type locality: Dieppe, English Channel) is a very large, solitary form (18 cm in height, 200 oral tentacles, 30 aboral tentacles). This is somewhat beyond the usual range of *T. indivisa*, but *T. insignis* is here nevertheless regarded as a likely conspecific with *T. indivisa*. It would also fit *T. regalis*, but this species has never been found so far south.

The status of *Tubularia couthouyi* L. Agassiz, 1862 is not entirely clear. Some of its unique features given in the original description of Agassiz (1862) are its hydranth size (diameter of tentacles crown 3.8 cm), and its occurrence in brackish water in groups of a few, tangled individuals. These characteristics do not separate it reliably from *T. indivisa*, but Fraser gives as distinctive trait the presence of regular nodes along the stem. Petersen (1990) regarded it as conspecific with *T. indivisa*. For biogeographic reasons it could nevertheless be regarded as valid and so I prefer to keep it as a questionable synonym only.

The identity of *Tubularia divisa* Osborn, 1893 is not clear, and perhaps the name is merely a spelling mistake.

Tubularia obliqua Bonnevie, 1898 and *Tubularia ceratogyne* Pérez, 1920 are both characterized by the tentacle-like appendix of the female sporosacs. Swenander (1904) and Broch (1915) indicated that such processes are variably present and that *T. obliqua* must be regarded as a synonym of *T. indivisa*. Hughes (1983) found that some

polyps of *T. indivisa* had both types of female sporosacs, an observation also made in the material observed for this study. Moreover, Hughes (1983) observed that the progeny of each type could change to the other form. *Tubularia ceratogyne* must thus be regarded as conspecific with *T. indivisa*. Petersen (1990) disagrees, forwarding differences in the arrangement of the gonophores on the blastostyle. These differences could not be observed in the material examined for this study and *T. ceratogyne* is regarded as conspecific with *T. indivisa*.

Tubularia indivisa var. *littoralis* Borowski, 1910 is a shallow water form of *T. indivisa*, while *Tubularia indivisa* var. *solitaria* Borowski, 1910 is a solitary form.

Tubularia indivisa var. *antarctica* Hartlaub, 1905 from South Georgia is for biogeographic reasons better regarded as a distinct species, thus it should be used as *T. antarctica* Hartlaub, 1905. Likewise, the inadequately described *Tubularia ornata* Couthouy, 1846 should not be synonymized with *T. indivisa* as has been suggested by Bedot (1905).

REMARKS: *Tubularia indivisa* and *T. regalis* can co-occur in the Arctic seas. *Tubularia regalis* is usually taller and has a larger hydranth than *T. indivisa*, but the size ranges of both overlap largely. For a reliable identification the mature female gonophores must be known as *Tubularia regalis* differs from *T. indivisa* by having meridional crests on its female sporosacs (see Fig. 3).

Tubularia regalis Boeck, 1860 Fig. 3

Tubularia regalis Boeck, 1860: 114, pl. 3. – Bonnevie, 1899: 28, pl. 1 fig. 5. – Swenander, 1904: 8, figs 4-5. – Broch, 1915: 4, pl. 1 1-6, pl. 2 fig. 7-10. – Broch, 1916: 25, fig. E. – Kramp, 1943: 7. – Calder, 1972: 222, pl. 1 fig. 3. – Petersen, 1990: 201. – Schuchert, 2001a: 45, fig. 31B.
? *Tubularia borealis* Clark, 1877: 231. – Calder, 1972: 222, possible synonym.
Tubularia variabilis Bonnevie, 1898: 471, pl. 25 fig 12. – Bonnevie, 1899: 26, pl. 1 fig. 4. – Swenander, 1904: 8, synonym. – Broch, 1915: 5, synonym.
? *Tubularia regalis*. – Thomson, 1909: 143.
in part *Tubularia indivisa*. – Naumov, 1969: 237, fig. 108.

MATERIAL EXAMINED: ZMUC, without registration number; Greenland, Cape Farewell; 250-400 m; collected 17.08.1970; 6 fertile polyps. – ZMUC, without registration number; Greenland, Kvanefjord, 290-400 m; collected 26.06.1912; det. P. Kramp; several polyps. – ZMUC, without registration number; Kara Sea; collected 1884; one polyp on bivalve; det. Bergh; identification is only tentative as juvenile, stem ends in basal plate. – ZMUC, without registration number; Sea of Japan; fertile; det. Petersen. – ZMUC, without registration number; between Faroe and Shetland Islands; 920 m; collected before 1890; several fertile polyps; det. Broch.

DIAGNOSIS: Like *Tubularia indivisa*, but female sporosacs with 3-7 meridional crests, stems taller 10-30 cm and thicker, hydranths larger, individual stems in smaller groups or single, restricted to cold Arctic waters and usually in deep waters.

DESCRIPTION: Hydroid solitary (not colonial), usually growing in characteristic clusters comprising 2-5 individuals with entwined basal parts of stems. Hydroid sometimes also occurs singly. Stems attached to substratum by unbranched, creeping stolons or a basal disc.

Stem length of fertile hydranths variable. Stem perisarc firm, regular annulations or nodes rare or absent but perisarc tube in lower part often irregular and gnarled. Coenosarc of stems with about 12 peripheral canals, one of them usually

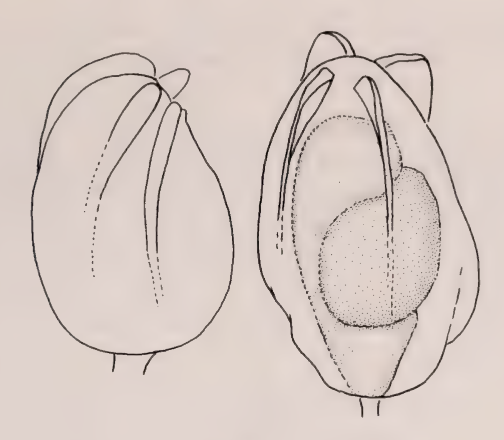


FIG. 3

Tubularia regalis Boeck, 1860; after preserved material from Greenland, two female gonophores, size about 1.2 mm.

larger, central region filled with loose parenchymatic cells. The canals give the stems a longitudinal striation pattern.

Neck region with inflated, filmy perisarc originating at junction of hydranth and caulus (thus neck without collar), neck region about as large as hydranth.

Hydranth flask-shaped, with one aboral whorl of 35-40 long aboral tentacles and 35-40 short oral tentacles in up to five closely set whorls, oral tentacles continued on hydranth body as longitudinal ridges. Proximal region of aboral tentacles laterally flattened, cross-section oval.

Gonophores borne on 10-20, long, unbranched blastostyles originating above aboral tentacles, shorter than aboral tentacles. Each blastostyle with up to 30 gonophores with a short pedicel, arranged along the whole length of the blastostyle, sometimes with a tendency to be arranged in two opposite rows. Gonophores remain fixed as sporosacs.

Female sporosacs ovate, with rounded distal end, opening subterminal, thus rendering symmetry bilateral, opening surrounded by 3-7 radiating crests (Fig. 3), shape and size variable. During development usually with 3-7 radial canals of unequal length and a circular canal, canals becoming reduced or invisible in mature stages, also crests usually reduced in fully mature gonophores. One egg per gonophore developing into actinula in situ. Male gonophores oval, smaller than female ones, at no stage with crests, radial canals or ring canal.

Nematocysts and colours unknown.

DIMENSIONS: Stem height of reproductive animals about 15-20, rarely 30 cm, stem diameter up to 3 mm. Aboral tentacles up to 4 cm long.

OTHER DATA: The development of the gonophores, especially of the radial canals, was examined by Broch (1915).

BIOLOGY: Rare, usually in deeper waters, except perhaps in the high Arctic, depth range approximately 50-900 m (Bonnevie, 1898; Christiansen, 1972; own data).

Broch (1915) reported that in the Trondheimsfjord it occurs especially on the bivalve *Lima excavata* on naked rocks, while Christiansen (1972) found it mainly on *Lophelia corals*.

DISTRIBUTION: Mainly an Arctic species, known from western and eastern Greenland, Spitsbergen, Norway, The Faroes, eastern Canada, Barents Sea, White Sea, Kara Sea (Bonnevie, 1898; Kramp, 1914, 1932; Broch, 1916; Christiansen, 1972; Schuchert, 2001a). Apparently absent from Iceland (Schuchert, 2001a). The southernmost record seems to be the northern tip of Scotland (Thomson, 1909), but the identity of the sample is unclear as its gonophores lacked the typical ridges. Otherwise, the southern limit of this species is the region of the Shetland and Faroes Islands and southern Norway (Christiansen, 1972). Type locality: Belsund, Spitsbergen.

REMARKS: *Tubularia regalis* is usually larger than *T. indivisa*, normally by about a factor of two, but their size ranges overlap. So, the only reliable character to distinguish both species is the morphology of the female gonophores. Only *T. regalis* has radiating crests on its female gonophores, although they are usually reduced in fully mature gonophores. Both species co-occur in the North Atlantic. Naumov (1969) regarded *Tubularia regalis* and *T. indivisa* as conspecific, but most contemporary authors considered them as valid (Calder, 1972; Petersen, 1990; Schuchert, 2001a).

Tubularia asymmetrica strongly resembles *T. regalis*, but has only three protuberances in the proximal half of the sporosac and male and female sporosacs occur on the same blastostyle.

Tubularia asymmetrica Bonnevie, 1898 Fig. 4

Tubularia asymmetrica Bonnevie, 1898: 472, pl. 25 figs 13-19. – Bonnevie, 1899: 25. – Swenander, 1904: 9.

TYPE MATERIAL EXAMINED: ZMO slides numbers B1354 through 1362, Rödberg, serial sections of sporosacs on blastostyles, male and female sporosacs present, female sporosacs of different developmental stages, some with oogonia, some with actinula larvae.

DIAGNOSIS: Like very large *T. indivisa* or *T. regalis*, male and female sporosacs on same blastostyle, female sporosacs with three lateral protuberances in proximal half.

DIMENSIONS AND OTHER DATA (Bonnevie, 1898): About 20 aboral tentacles 3-4 cm long, oral tentacles 4-6 mm; stem diameter distal 2 mm tapering towards basal to 1 mm; 8-16 blastostyles, female sporosacs initially with three radial canals, these later reduced, three basio-lateral protrusions are homologues of marginal bulbs.

DISTRIBUTION: Known only from type locality, Rødberg Trondheimsfjord, Norway (Bonnevie, 1898; Swenander, 1904).

REMARKS: This species has been seen only by Bonnevie (1898) and Swenander (1904). It has female sporosacs with three lateral tubercles in its lower half (Fig. 4B) and is otherwise very similar to *T. regalis*. The only tangible difference to this species is the occurrence of male and female sporosacs on the same blastostyle. This is not necessarily a diagnostic character as hermaphroditism is also well known for other Tubulariidae (see *E. crocea* and *E. larynx*) and might have gone unnoticed in the few

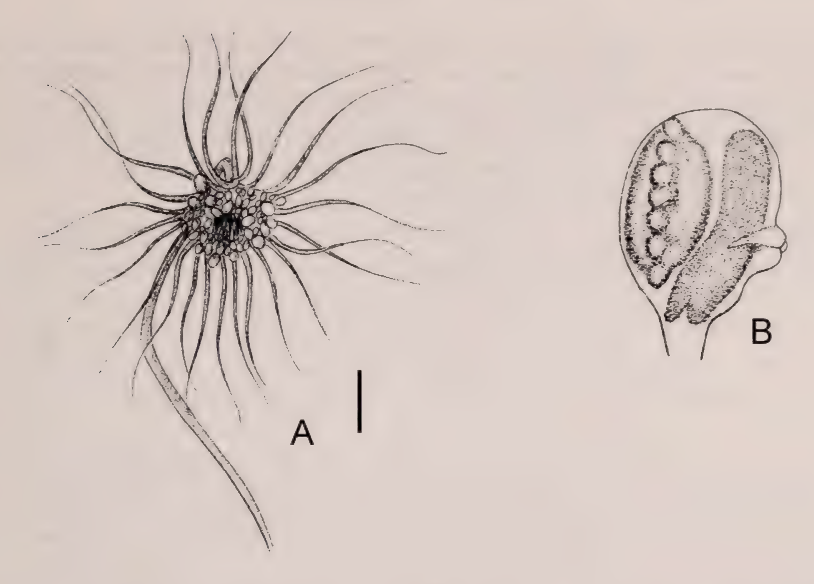


FIG. 4

Tubularia asymmetrica Bonnevie, 1898, modified after Bonnevie (1898). (A) Single polyp without basal part, scale bar 1 cm. (B) Female sporosac in side-view, note the characteristic three lateral protuberances, an actinula is visible inside.

specimens of *T. regalis* found so far. A re-examination of the remaining type material of *T. asymmetrica* confirmed the observations of Bonnevie, but did not add new information. The female sporosacs (two examined) indeed have three bumps in their lower half. One of them is larger and at least in younger stages with a transient radial canal connecting it to the spadix. The protuberances are thus likely vestiges of marginal bulbs.

The species must be redescribed based on new material.

Genus ***Ectopleura*** L. Agassiz, 1862

Vorticlava Alder, 1856a; type species *Vorticlava humilis* Alder, 1856a by monotypy, synonym of *E. larynx*.
Thamnocnidia Agassiz, 1860; no type species designated yet.
Parypha Agassiz, 1860; no type species designated yet.
Ectopleura L. Agassiz, 1862; type species *Tubularia dumortierii* van Beneden, 1844 by designation by Mayer (1910).
Acharadria Wright, 1863a; type species *Acharadria larynx* Wright, 1863a by monotypy [= *Ectopleura wrighti* Petersen, 1979].
Paripha Agassiz, 1865. [incorrect spelling]
Acharadrium Allman, 1872. [incorrect spelling]
Parhypha Delage & Hérouard, 1901. [incorrect spelling]
Acharadia Brinckmann-Voss, 1970. [incorrect spelling]
Parytha Fey, 1970. [incorrect spelling]
Pinauay Marques & Migotto, 2001; type species *Tubularia larynx* Ellis & Solander, 1786 by original designation.

DIAGNOSIS: Solitary or colonial Tubulariidae, hydranths vasiform with one whorl of oral and one whorl of aboral tentacles. Periderm on stem thin, covering pyri-

form neck region and secreted from circular groove around broadest part of neck, upper part of neck thus free of perisarc (neck with collar). Hydrocaulus hollow, with two, rarely up to five, longitudinal gastrodermal ridges, may be fused in centre by thin lamellae. Stolons creeping, tubular or forming dense net. Gonophores arise on blastostyles developing above aboral tentacles, dichotomously branched or not. Gonophores develop into free medusae, medusoids, or fixed sporosacs.

Medusa where present with evenly rounded umbrella, bell margin not oblique, exumbrella with eight meridional nematocyst tracks issuing in pairs from tentacle bulbs. With either two opposite or four perradial tentacles, moniliform or with abaxial nematocyst clusters. Four radial canals. Manubrium short, at most reaching bell margin, gonads encircle manubrium. Medusa in some species reduced to radially symmetrical medusoids or sporosacs with or without symmetrically arranged distal protuberances.

REMARKS: Marques & Migotto (2001) made a phylogenetic analysis of the Tubulariidae and found that the genus *Ectpleura* sensu Petersen is monophyletic, but composed of two distinct subclades. This made them propose to split the genus into two separate genera, *Ectopleura* sensu stricto and *Pinauay*. I can see no advantage why the monophyletic genus *Ectpleura*, which contains only a limited number of species, should be split up. Because *E. larynx* was selected as type species for *Pinauay*, this introduction would again require unwelcome name changes for rather common species like *E. larynx* or *E. crocea*. Moreover, *Pinauay* is a junior synonym of *Vorticlava* Alder, 1856a and potentially also of *Thamnocnida* Agassiz, 1860, and *Parypha* Agassiz, 1860. All three names actually have precedence over *Ectopleura*, but after Allman (1872) synonymized them they have been seldom used during the last century, while *Ectopleura* is a well-established name (ICZN Art. 23.9.1).

For a list of all *Ectopleura* species see Bouillon *et al.* (2006).

KEY TO SPECIES OF *ECTOPLEURA* POLYPS OF THE ERMS ZONE:

1a	gonophores liberated as medusae with tentacles	3
1b	gonophores fixed sporosacs	2
2a	female sporosacs usually with four short, tentacle-like processes, only one egg-like mass or embryo per sporosac, tightly packed	*E. larynx*
2b	female sporosacs with 6-8 crest-like processes around distal opening, 2-4 egg masses or embryos per sporosac, loosely packed	*E. crocea*
3a	stem small (1 cm), maximally 16 aboral tentacles, with somewhat capitate oral tentacles, advanced medusa buds with two tentacles	*E. wrighti*
3b	stem > 1 cm, more than 16 aboral tentacles, oral tentacles filiform, advanced medusa buds with four tentacles	*E. dumortierii*

KEY TO SPECIES OF *ECTOPLEURA* MEDUSAE OF THE ERMS ZONE:

1a	manubrium with four perradial, sac-like pouches	*E. sacculifera*
1b	manubrium without pouches	2
2a	with two opposite tentacles	*E. wrighti*
2b	with four tentacles	*E. dumortieri*

Ectopleura larynx (Ellis & Solander, 1786) Fig. 5

Tubularia larynx Ellis & Solander, 1786: 31. – Allman, 1872: 406, pl. 21, synonymy. – Nutting, 1901: 338, fig. 17. – Fenchel, 1905: 507, plates 10-12, revision, synonymy. – Broch, 1911: 13, fig. 10, pl. 2 fig. 2. – Broch, 1916: 27, Fig. F. – Vervoort, 1946: 103, figs 39b & 41. – Ralph, 1953: 68, fig. 12. – Hawes, 1955: 333, figs 1-5. – Naumov, 1969: 239, fig. 109. – Brinckmann-Voss, 1970: 31. – Miller, 1973: fig. A & E, not B. – Millard, 1975: 35, fig. 15H-J. – Werner, 1984: fig. 106. – Cornelius *et al.*, 1990: 116, fig. 4.5. – Östman *et al.*, 1995: 165, figs 1-45.

not *Acharadria larynx* Wright, 1863: 378, pl. 17 figs 7-8. [= *Ectopleura wrighti* Petersen, 1979]

Tubularia muscoides Pallas, 1766: 82. [not *Tubularia muscoides* Linnaeus, 1761 = *Coryne muscoides*]

Tubularia coronata Abildgaard, 1806: 25, pl. 141. – Hincks, 1868: 119, pl. 21 fig. 2. – Fenchel, 1905: 573, synonym. – Weill, 1934: 365, figs 39a-b, 185a, 211

Tubularia pygmea Lamouroux, 1816: 252. – Fenchel, 1905: 573, synonym.

Eudendrium bryoides Ehrenberg, 1834: 296. – Hincks, 1868: 118, synonym.

Tubularia polyceps Dalyell, 1835: 601. – Fenchel, 1905: 573, synonym.

Tubularia gracilis Harvey, 1836: 54. – Hincks, 1868: 119, synonym.

Vorticlava humilis Alder, 1856a: 353, pl. 12 figs 1-4. – Alder, 1857a: 100, pl. 3 figs 1-4. – Weill, 1934: 370, fig. 219, synonym. – Cornelius & Garfath, 1980: 276, type material.

Thamnocnidia spectabilis L. Agassiz, 1862: 271, pl. 22 figs 1-20. – Fenchel, 1905: 573, synonym.

Thamnocnidia tenella L. Agassiz, 1862: 275, pl. 22 figs 21-30. – Fenchel, 1905: 573, synonym.

? *Tubularia simplex* Alder, 1862: 232, pl. 8 figs 3-4. – Hincks, 1868: 121, pl. 22 fig.1. – Naumov, 1969: 237, fig. 107. – Cornelius & Garfath, 1980: 275, type material.

Tubularia bellis Allman, 1863: 12. – Hincks, 1868: 122, pl. 21 fig. 3. – Allman, 1872: 409, pl. 22 figs 5-6. – Fenchel, 1905: 573, synonym. – Hawes, 1955: 341, synonym

Tubularia humilis Allman, 1864b: 60. – Hincks, 1868: 3. – Allman, 1872: 411, pl. 22 figs 3-4. – Fenchel, 1905: 573, synonym. – Hawes, 1955: 341, synonym.

Tubularia attenuata Allman, 1864b: 60. – Hincks, 1868: 122. – Allman, 1872: 410, pl. 22 figs 1-2. – Hawes, 1955: 341, synonym.

Thamnocnidia tubularoides A. Agassiz, 1865: 196. – Fenchel, 1905: 573, synonym.

Tubularia pacifica Allman, 1872: 416, new name for *T. tubularoides* Agassiz. – Fenchel, 1905: 573, synonym.

Tubularia polycarpa Allman, 1872: 413. – Fenchel, 1905: 573, synonym. – Hawes, 1955: 341, synonym.

? *Tubularia attenoides* Coughtrey, 1876: 302.

? *Tubularia britannica* Pennington, 1885: 75, pl. 3 fig 8.

Parytha larynx. – Fey, 1970: 389. [incorrect spelling]

Ectopleura larynx. – Petersen, 1990: 170. – Schuchert, 1996: 109, fig. 65a-b. – Calder & Vervoort, 1998: 10, fig. 3. – Bouillon *et al.*, 2004: 105, fig. 56A-B.

in part *Ectopleura larynx*. – Schuchert, 2001a: 43, fig. 30A-E.

Type material examined: ZMUC, syntype material of *T. attenoides* Coughtrey, 1876, New Zealand, Dunedin, Otago Heads, ex. British Museum no. 1886.11.17.2.

Other material examined: MHNG INVE 64052; France, Normandie, Luc-sur-Mer; collected 24.08.1988, fertile females. – MHNG INVE 34657, The Netherlands, the Helder, coll. 1897; fertile males and females. – MHNG INVE 34659, France, Roscoff, tonne du Pot de Fer, coll 16.05.1910, fertile; on seaweed, stems very short 1 cm, material of Bedot (1911). – MHNG INVE 29389, France, Brittany, Bay of Morlaix, St. Pol de Léon; ca. 20 m depth; coll. 5 Jun 2000; on *Ciona intestinalis*; fertile; 16S sequence **AY787877**. – MHNG INVE 62576; Norway, Raunefjord, Vatlestraumen; 60.380°N 05.182°E; depth 30-50 m; collected 18.09.2008; on *Grammaria abietina*; fertile male; *E. bellis* form; 16S **FN687536**. – MHNG INVE 62575; Norway, Raunefjord, Flesland, 60.292°N 05.183°E; depth 6-8 m; collected 18.09.2008; on red algae; incipient sporosacs present; *E. bellis* form (size 1 cm); 16 S **FN687537**. – MHNG INVE 34781, as *Tubularia bellis*, Monaco, coll. February 1902, fertile. – MHNG INVE 34434; France, Marseille, inlet of ship cooling-system, coll. H. Zibrowius, 07.03.2003. – BMNH 1948.10.1.17; as *T. bellis*; Great Britain, Isle of Man; collected 04.04.1894; fertile; coll. E. Browne. – BMNH

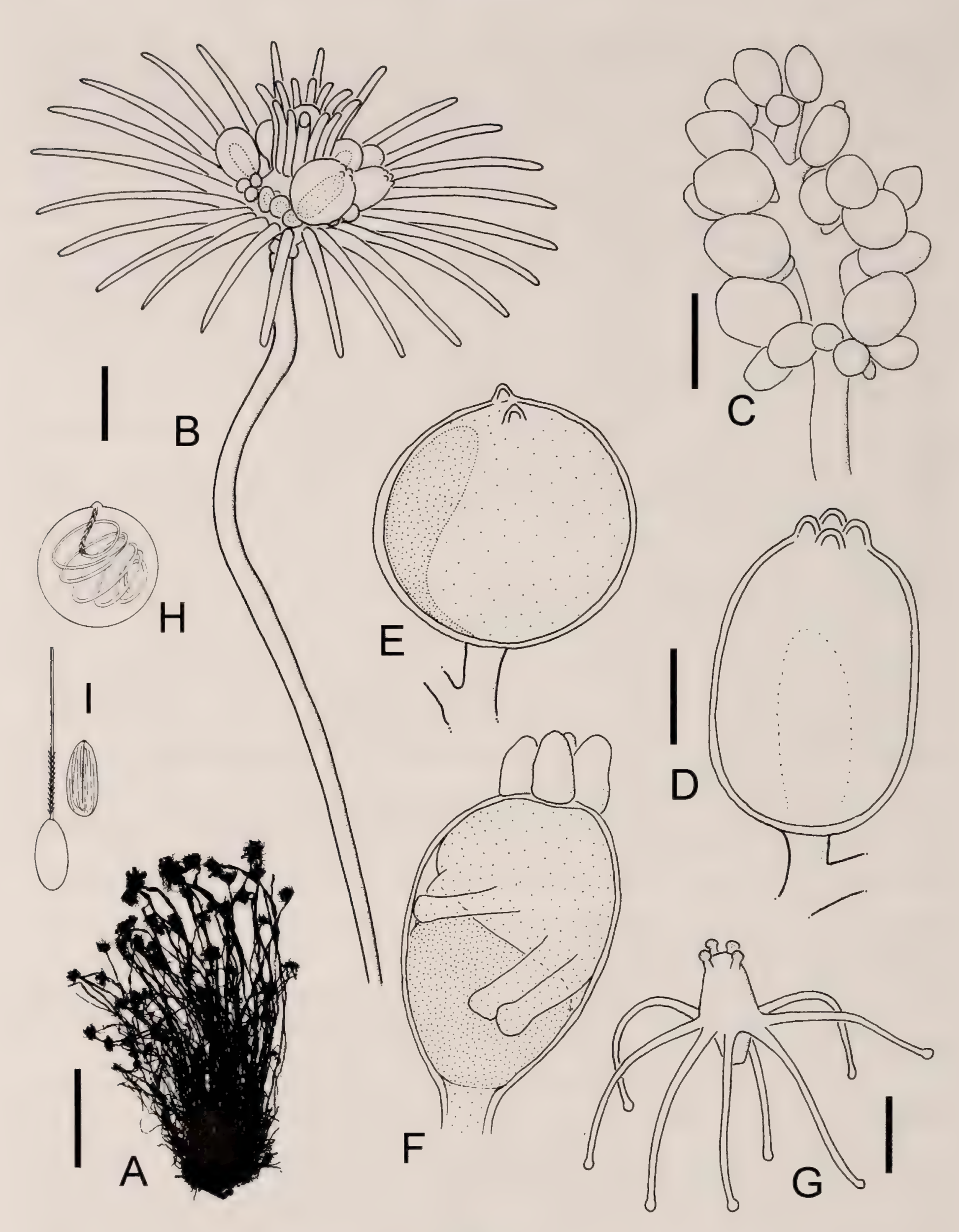


FIG. 5

Ectopleura larynx (Ellis & Solander, 1786); A after Dutch material; B, D & E after living material from Roscoff; C after MHNG INVE 34659; H-I from Weill (1934). (A) Silhouette of part of colony, scale equals 2 cm. (B) Subadult hydranth with beginning gonophore maturation, scale equals 1 mm. (C) Fully grown blastostyle with male sporosacs, scale bar 0.5 mm. (D-F) female gonophores, note variability of tentacle-like processes, in F a developing actinula is present within the sporosac, scale bar 0.2 mm. (G) Newly hatched actinula, scale bar 0.5 mm. (H) Undischarged spherical basitrichous isorhiza, diameter 10-12 μm. (I) Discharged and undischarged oval basitrichous isorhizas, about 10x5 μm.

1948.10.1.16; as *T. bellis*; Great Britain, Isle of Man, Port Erin; collected 1893; fertile; coll. E. T. Browne. – MHNG INVE 54563; England; Plymouth, Firestone Bay; depth 20 m; collected 05.05.2007; on *T. indivisa*; fertile, stem size 2-5 cm; 16S **FN687535**. – BMNH 1972.11.29.1; as *T. bellis*; Ireland, Lough Ine; fertile; badly preserved, det. J. A Kitching, female sporosacs without 4 processes. – BELUM Md 454; Ireland, Wexford, Saltee Islands, Coningbeg Rock, 52.0678°N 06.6408°W; depth 30 m; collected 26.05.1982; on *T. indivisa*. – BELUM Md96; Northern Ireland, Down, Strangford Lough, Ballyhenry Bay, 54.3875°N 05.5617°W; depth 9 m; collected 27.06.1980; male; includes *T. bellis* form. – ZMUC, no registration number; Canada, Nova Scotia, Chester Basin; collected 01.12.1970; fertile. – Mediterranean, Banyuls-sur-Mer, south of Anse de Troc; depth 2 m; collected 11.05.2002; on barnacles; *T. bellis* form; fertile male; no material preserved; 16S **FN687538**. – Mediterranean, France, Calanque du Port d'Alon, 43.14475°N 5.707861°E; depth 1 m; collected 22.04.2003; *T. bellis* form; on rock; fertile female; no material preserved; 16S **FN687539**.

DIAGNOSIS: *Ectopleura* with sporosacs lacking radial canals at all stages, female sporosacs usually bearing four short, tentacle-like processes, only one egg-like mass or embryo per sporosac.

DESCRIPTION: Colonial tubulariid hydroids, arising from ramified stolons. Colonies usually large and dense, forming a tangled mat of loose stolons and basal stem parts; solitary hydranths can occur. Stems not regularly branching, but with apparent branching by settling of larvae on stems of older polyps, stem diameter equal throughout or only slightly increasing towards distal, bases of stems not bundled or entwined as in *E. indivisa*. Perisarc of stem thin, with some irregular annulations which may be more or less pronounced, especially short-stemmed forms have regular nodes. Neck region below hydranth with groove from which a filmy perisarc which is secreted, this groove at some distance from distal end of neck region, thus forming a collar. Coenosarc in stem with 2-4 longitudinal ridges projecting into lumen or ridges fused in centre. Hydranth vasiform with long hypostome, generally slightly more aboral than oral tentacles, with one oral whorl of 14-28 filiform tentacles adnate to hypostome, one aboral whorl of about 16-29 long, filiform tentacles, aboral tentacles laterally compressed. Gonophores born on blastostyles that may be branched or not, if branched with up to four ends. Blastostyles arising above aboral tentacles, 12-16 per hydranth (range 5-35), sometimes in two whorls when present in high numbers, reaching a length like the one of the tentacles, usually shorter, with 10-20 gonophores.

Gonophores remain fixed as sporosacs, oval to spherical, without radial canals, with red spadix. Mature female gonophores radially symmetric with four tentacle-like processes around opening at distal end, form of processes very variable, occasionally reduced or absent. Spadix can protrude out of sporosac opening, opening is terminal. Aging female hydranths becoming hermaphroditic. Female sporosacs filled with numerous small cells forming an egg-like mass and leaving no empty space, no distinct oocytes and no visible pronuclei. Only one embryo develops inside female gonophore, filling gonophore entirely (Fig. 5F). Actinula larva after hatching with or without four oral capitate tentacles and about eight aboral tentacles with swollen ends. Male gonophores more oval, with a distal thickening of epidermis, no processes.

Colours: spadix and hydranth base reddish.

Nematocysts: three size classes of stenoteles, desmonemes, oval and spherical microbasic basitrichous isorhizas (Fig 5H-I), rare euryteles (for details see Östman *et al.*, 1995; note that they call the oval izorhizas "pseudo-mastigophores").

Dimensions (reproductive animals): Stems 1-17 cm high, length very variable even within same cluster, diameter of stems about 0.5 mm. Diameter of hydranth at level of aboral tentacles about up to 2 mm. Contracted aboral tentacles about 2 mm long. Sporosacs 0.5-0.7 mm. For detailed measurements of the nematocysts see Östman *et al*. (1995) and Weill (1934, as *T. coronata*).

Variation: Fenchel (1905) and Hawes (1955) provide very useful data on the variability of this species.

Other data: Fenchel (1905), Pérez (1925), and Hawes (1955) found that aging female polyps develop male sporosacs. Usually the most distal sporosacs of a blastostyle produces male gametes, while the others remain female. Hamann (1882, in part as *T. coronata*) and Lowe (1925) examined the embryology and histology of the hydranths.

Biology: Usually found in depths of 1-30 m, but records down to 3000 m are known (Bonnevie, 1899; Fey, 1970; Christiansen, 1972; Calder & Vervoort, 1998; Schuchert, 2001a). *Ectopleura larynx* tolerates reduced salinity at least down to 18 ppt (Schönborn *et al*., 1993). In the Atlantic, reproduction usually takes place from May to October (Pyefinch & Downing, 1949; Hamond, 1957; Christiansen, 1972; own observations). The generation time is about 24 days (Pyefinch & Downing, 1949). In the Mediterranean, the reproductive period is from November to May (Motz-Kossowska, 1905; Boero & Fresi, 1986; own observations). The developmental biology has been investigated by Allman (1871), Lowe (1925), Hawes (1955), and Afzelius (1971). Aspects of its ecology and behaviour have been investigated by Pyefinch & Downing (1949), Schmidt (1983), Orlov (1994), and Nellis & Bourget (1996). Gili *et al*. (1996) analyzed its feeding behaviour.

Distribution: Circumglobal in temperate and cold waters, but many records are unreliable as not based on fertile females. May be transported as a fouling organism on ships. It is common along European costs of the Atlantic from the Arctic to the Iberian Peninsula, the Baltic Sea, but less frequent in the Mediterranean (e. g. Hincks, 1868; Bonnevie, 1899; Fenchel, 1905; Motz-Kossowska, 1905; Jäderholm, 1909; Broch, 1916; Robson, 1914; Billard, 1927; Kramp, 1942; Vervoort, 1946; Leloup, 1947; Hamond, 1957; Teissier, 1965; Rees & Rowe, 1969; Fey, 1970; Patriti, 1970; Christiansen, 1972; Schönborn *et al*., 1993; Medel & López-González, 1996; Schuchert, 2001a). Type locality: British Isles (Ellis, 1755).

Remarks: The synonymy of this species has been elaborated in detail by Fenchel (1905). Others, e. g. Péréz (1925), Hawes (1955) and Petersen (1990), also commented on its synonymy and their view is adopted here. Fenchel (1905) and Hawes (1955) also included *Tubulia bellis* Allman, 1863 in the synonmy of *E. larynx*. Cornelius *et al*. (1990), however, regarded it as valid, without giving arguments. According to Allman (1872), *E. bellis* differs from *E. larynx* by its short stems (up to 2.5 cm) and the more pronounced corrugation of the perisarc. Specimens matching these criteria were also examined during this study (see Material Examined) and it was also found in assemblages that were otherwise attributable to *E. larynx*, although the distinction of the two forms was often arbitrary as they intergrade. The 16S sequences of the bellis-form and the normal form showed no significant sequence differences. In

view of the enormous variability of the stem height, I thus concur with Fenchel (1905) and Hawes (1955) that *T. bellis* Allman, 1963 is likely only a small form of *E. larynx* and that they cannot objectively be separated. Stem lengths in *Ectopleura* species depend very much on environmental conditions (Hawes, 1955).

The status of *Tubularia simplex* Alder, 1862 is likewise unclear (Cornelius & Garfath, 1980). Vervoort (1946) referred it to *E. larynx*, but Naumov (1969) kept it separate, although it is not entirely evident on what he based his distinction. The species was based on infertile material and the only useful taxonomic characters are the oral tentacles disposed in two circlets and the solitary occurrence. These characters are rather suggestive of *Hybocodon prolifer*, but a correct identification will presumably never be possible, as for the many other nominal species listed in the synonymy above.

Tubularia attenoides Coughtrey, 1876 from New Zealand was referred to *E. larynx* in one of my earlier publications (Schuchert, 1996). Meanwhile, I was able to examine type material of this nominal species. This material appears indistinguishable from *E. larynx* as described above, with one important exception: the four distal processes of the female gonophore are not tentacle-like but leaf-like and resemble those of *E. crocea*. In younger gonophores they are more nipple-like. Whether this difference is sufficient to keep *E. attenoides* distinct from *E. larynx* cannot be decided yet. The subtle difference might also be due to geographic variation. The species herein is therefore considered questionably conspecific with *E. larynx*.

Allman (1872) states that *E. larynx* produces an actinula lacking oral tentacles at the time of liberation. This could not be confirmed in the present material (Fig. 5G) and also other authors observed actinulae with oral tentacles (Werner, 1984; Petersen, 1990).

Ectopleura larynx and *E. crocea* have often been confounded. Both species resemble each other very closely and only the ornaments of female gonophores allow a secure distinction. It appears also that the number of actinula larvae per gonophore is characteristic, with *E. larynx* having only one and *E. crocea* up to three. In *E. larynx*, the actinula completely fills the sporosac, while in *E. crocea* some empty space may remain. The hydranths of *E. crocea* are usually larger than those of *E. larynx*, but this is not a reliable diagnostic character to identify infertile material.

Ectopleura crocea (L. Agassiz, 1862) Fig. 6

Parypha crocea L. Agassiz, 1862: 249, pls 23-23a.

Tubularia crocea. – Allman, 1872: 416. – Nutting, 1901: 340, fig. 19. – Torrey, 1902: 43, pl. 3 figs 22-23. – Weill, 1934: 367, fig. 213. – Fraser, 1937: 51, pl. 9 fig 41. – Fraser, 1944: 97, pl. 17 fig. 70. – Rees, 1963: 1223. – Brinckmann-Voss, 1970: 28, figs 30-34. – Miller, 1973: fig. C & F (legend incorrect). – Tardent, 1978: 277, figs 107-108. – Morri, 1981: 56, fig. 17, pl 1 figs 1 & 11, pl. 2 fig. 1. – Morri & Boero, 1986: 28, figs 9-10.

Tubularia mesembryanthemum Allman, 1872: 418, figs 83-84. – Hirohito, 1988: 18, fig. 4, pl. 1 fig. B. – Weill, 1934: 369.

not *Tubularia mesembryanthemum*. – Franzen & Hündgen, 1986: 401, figs 1-34. [= *E. wrighti*]

Tubularia polycarpa Allman, 1972: 413. – Rees, 1963: 1224, synonym.

Tubularia Ralphi Bale, 1884: 42. – Watson, 1980: 60, figs 25-37. – Schuchert, 1996: 109. **new syn.**

Tubularia gracilis von Lendenfeld, 1885: 597, pl. 27 figs 51-52. **new syn.** [not *T. gracilis* Harvey, 1836, = *E. larynx*]

Tubularia australis Stechow, 1924: 57. **new syn.**

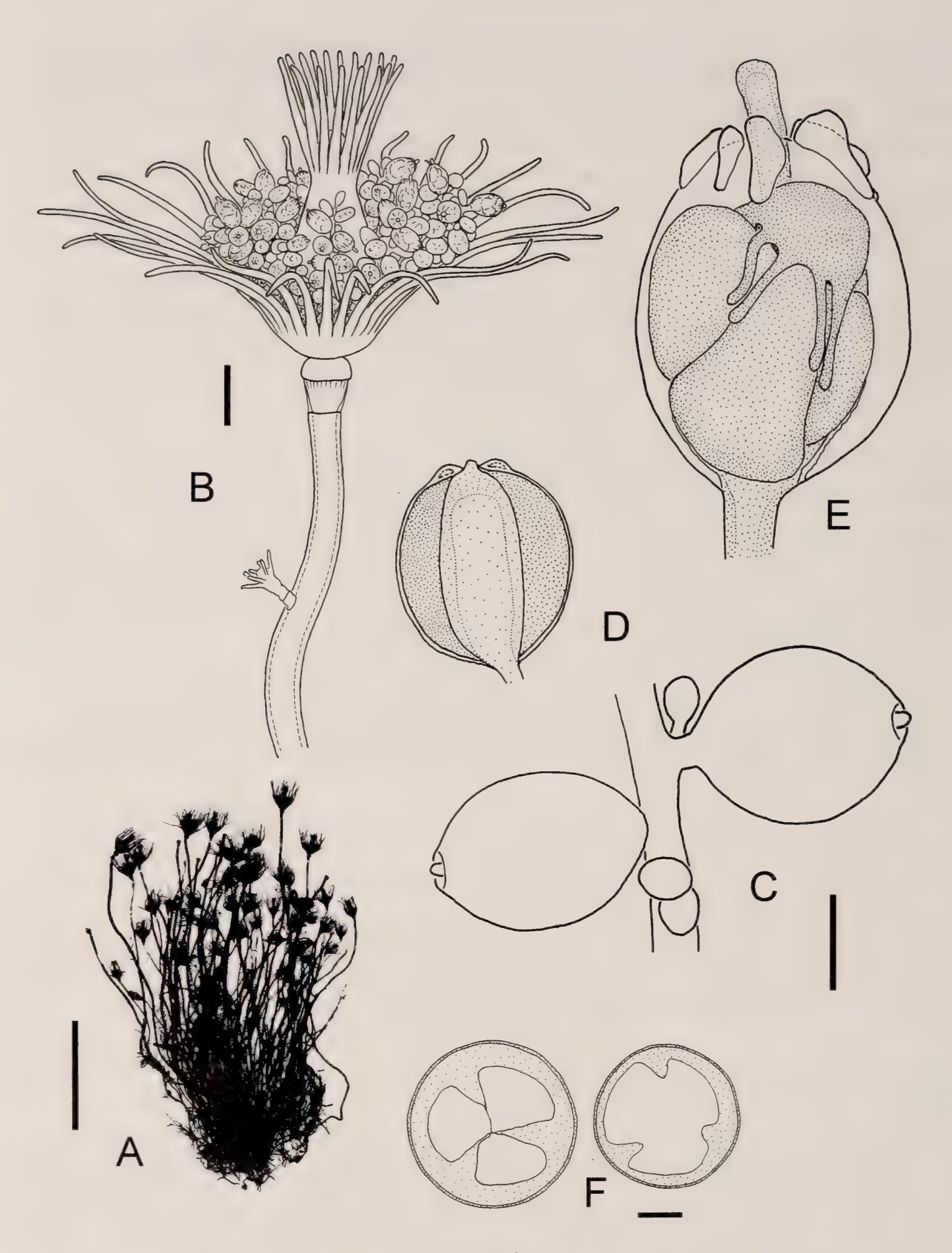


FIG. 6

Ectopleura crocea (L. Agassiz, 1862), all after preserved material from the Mediterranean. (A) Colony silhouette, scale bar 2 cm. (B) Hydranth and part of stem, note young settler on stem, scale bar equals 2 mm. (C) Part of blastostyle with male sporosacs, scale equals 0.2 mm. (D) Optical section of a younger male sporosac with four shallow bumps encircling opening, note that these elevations are not always present or visible, same scale as C. (E) Female sporosac containing an actinula and embryos; note the presence of the characteristic processes encircling the distal opening, the spadix protrudes from the opening, same scale as C. (F) Schematic cross-sections of a stem, left in distal region, right in more basal region, scale bar 0.2 mm.

? *Tubularia sagamia* Stechow, 1908a: 194. – Stechow, 1909a: 43, pl. 3 fig. 6, pl. 5 fig. 5, pl. 6 figs 22-25.
Tubularia warreni Ewer, 1953: 351, figs 1-4. – Millard, 1975: 35, fig. 15A-G, frontispiece. **new syn.**
Ectopleura crocea. – Petersen, 1990: 174, fig. 27. – Schuchert, 1996: 64a-g. – Bouillon *et al*., 2004: 104, fig. 55E-F.
in part *Ectopleura larynx*. – Schuchert, 2001a: fig. D.

Type material examined: Neotype of *T. ralphii*, Museum of Victoria; Victoria, Hobson Bay, Yarra river entrance, depth 1-2m, on *Mytilus edulis* and *Styela clava*; collected 03.04.1977 by J. Watson.

Nontype material: MHNG INVE 34010; South Africa, Langebaan, mass occurrence on floating pier; depth 0 m; 10.01.2003; female & male colonies; 16S sequence **FN687540**. – MHNG INVE 25844; USA, South Carolina, Charleston Harbor; depth 12 m; 02.01.1975; female and male hydranths; leg. D. Calder. – MHNG INVE 34758; USA, Massachusetts; male. – MHNG INVE 64208; USA, North Carolina, Beaufort; male colony; collected October 2000 by A. Lindner; 16 S determined by A. Lindner for PEET program, identical to **FN687540**. – MHNG INVE 34658; Italy, Naples; fertile. – MHNG INVE 34734; Italy, Naples; 18.04.1900; female. – MHNG INVE 34755; France, Villefranche-sur-mer; coll. 1895; male. – MHNG INVE 25959; France, Sète; 23.07.1980; female – MHNG INVE 34759; Italy, Naples; 9.03.1902; female and male polyps. – MHNG INVE 34766; Italy, Naples; 02.02.1892; male. – MHNG INVE 34771; Italy, Naples; 08.02.1892; female.

Diagnosis: *Ectopleura* with sporosacs lacking radial canals at all stages, female sporosacs usually bearing six to eight crest-like processes around distal opening, several eggs or embryos per sporosac.

Description: Colonial tubulariid hydroids arising from ramified stolons. Colonies large and dense, forming a tangled mat of loose stolons and basal parts of stems. Stems not regularly branching, but with apparent branching through settling of larvae on stems of older polyps. Bases of stems not bundled or entwined as in *E. indivisa*, stem diameter nearly equal throughout or doubling towards distal. Perisarc of stem below neck firm, with some irregular annulations which may be more or less pronounced. Neck region below hydranth with groove from which a filmy perisarc is secreted, this groove at some distance from distal end of neck region, thus forming a collar. Coenosarc of stem with 2-4 longitudinal ridges projecting into lumen (lower part of stem) or fused in centre by thin lamella (upper part), ridges visible exteriorly as 2-4 longitudinal lines. Hydranth vasiform with long hypostome, one oral whorl of about 18 (max. 26) filiform tentacles, adnate to hypostome, one aboral whorl of 22-28 (max. 38) long, filiform tentacles, aboral tentacles laterally compressed, four-sided. Gonophores born on blastostyles that are usually unbranched, but some branching can occur. Blastostyles arising distal to aboral tentacles, 12-16 per hydranth, variably developed, reaching a length like the tentacles, usually shorter, occasionally branched, with up to 20 gonophores of variable developmental stages.

Gonophores remain fixed as sporosacs, without radial canals, with club-shaped spadix, thin end of spadix often protruding. Individual hydranths usually of one sex, but aging females may develop additional male sporosacs. Female sporosacs oval, older female gonophores with 6-8 (rarely 10) distal processes, form variable but usually crest-like, occasionally reduced or absent. Development of embryo to actinula takes place inside sporosac. When mature, usually several eggs or embryos per sporosac (2-4), more loosely packed than in *E. larynx* (Figs 5F & 6E). Hatching

actinula larva with or without four short, capitate oral tentacles and 8-10 aboral tentacles with swollen ends. Male sporosacs smaller, with a distal thickening of epidermis, without crests like in females, but sometimes distal end bearing four shallow bumps.

Colours: spadix and hydranth base reddish.

Nematocysts: Stenoteles of two size classes, desmonemes, microbasic mastigophores, isorhizas, rare euryteles (Weill, 1934; Bouillon, 1974a; Schuchert, 1996).

DIMENSIONS: Stems 3-8 cm high (max. 12 cm, length very variable even within same cluster), stem diameter up to 2 mm, more usually 0.6-0.8 mm. Hydranth diameter at level of aboral tentacles up to 2.5 mm. Contracted aboral tentacles about 4 mm long. Female sporosacs 0.8 mm long and 0.6 mm wide. Nematocyst sizes, see Schuchert (1996) or Millard (1975, as *T. warreni*).

VARIATION: The morphological variability of *E. crocea* from various Egyptian localities was examined by Shoukr & Abdel-Hamid (1987).

BIOLOGY: *Ectopleura crocea* occurs in shallow waters from the low water level to about 30 m. The species mostly grows on ship hulls, buoys or other floating, man-made objects, also in quite polluted waters of harbours and lagoons. It often occurs also in estuarine conditions. The ability to grow on ship hulls, viz. the potential to be transported to other regions, may explain the circumglobal distribution of this species.

In the Mediterranean, fertile colonies occur throughout the year (Brinckmann-Voss, 1970). The feeding biology and diet is described by Genzano (2005).

The hydranths detach very easily upon mechanical disturbance (wave action). Rungger (1969) interpreted this autotomy as part of the life cycle and that it perhaps substitutes a free medusa stage (but see opposing view by Hughes, 1983).

Liu & Berrill (1948) and Berrill (1952) observed hermaphrodites in aging females.

DEVELOPMENT: The morphology and development of the gonophores as well as the early development are described by Hamann (1882) and Benoît (1921, 1925). Boelsterli (1975) describes the oogenesis with electron-optic methods. Brinckmann-Voss (1970) and Tardent (1978) depict the development of the actinula. Aspects of the larval biology have been documented by Yamashita *et al.* (1997, 2003).

DISTRIBUTION: Circumglobal in temperate waters, but many older records are unreliable as they are not based on female colonies (Petersen, 1990), likely distributed by human activity. In Europe usually rare, occasionally or locally more abundant, ranging from England (Browne, 1897; Rees, 1963), France (Teissier, 1965), Spain (Medel & López-González, 1996), Azores (Cornelius, 1992), and the Mediterranean (Brinckmann-Voss, 1970; Morri, 1981; Bouillon *et al.*, 2004). Type localities: Boston Harbour, USA.

SYNONYMY: *Ectopleura crocea* and *E. larynx* resemble each other closely and only fertile female colonies are reliably identifiable. For more details see under *E. larynx*.

Brinckmann-Voss (1970) is here followed in synonymizing *Tubularia mesembryanthemum* Allman, 1872 with *Ectopleura crocea* (L. Agassiz, 1862). No significant difference could be found in the material from the USA and the Mediterranean.

Watson (1980) redescribed *Tubularia ralphi* Bale, 1884 and designated a neotype. In the synonymy of *Tubularia ralphi* she also included *Tubularia gracilis* von Lendenfeld, 1885, *T. australis* Stechow, 1924 and *Tubularia warreni* Ewer, 1953, and *T. larynx* Ellis & Solander, 1786. Petersen (1990) followed her in this, with the exception of *T. larynx*, which is certainly distinct. I agree with Dr Watson, that *T. australis* Stechow, 1924 (a new name for the preoccupied name *T. gracilis* von Lendenfeld, 1885) and *T. warreni* are not objectively separable from *T. ralphi*. However, *T. ralphi* is also not reliably distinguishable from *Ectopleura crocea*. Petersen (1990) kept them distinct on account of the following differences: fewer tentacles (16-25 versus 22-30), branched blastostyles, and an actinula which has rudimentary oral tentacles when it is released. Schuchert (1996) re-examined the neotype of *T. ralphi* and found that the blastostyles are only occasionally branched, a trait also observed in *E. crocea* from the USA. Considering the general variability of the tentacle numbers in *E. crocea*, the difference observed by Petersen (1990) appears also insignificant. Therefore, only the difference of the actinula remains. Brinckmann-Voss (1970) described the newly hatched actinula as devoid of oral tentacles, but Tardent (1978: fig. 107e), who also worked with Mediterranean material, found that his animals produced actinulae with oral tentacles. Using the material available for this study, some actinulae were dissected out of their sporosacs. Three of them originating from material of the USA indeed had no oral tentacles, but one of four from the Mediterranean had small, but distinct oral tentacles. The presence of oral tentacles is thus also variable in *E. crocea* (and likely also *E. larynx*). This is not very surprising, as the oral tentacles will develop anyway immediately after the release of the actinula and the presence or absence in liberated ones is thus only a matter of timing. I therefore regard *Tubularia ralphi* as conspecific with *E. crocea*.

Tubularia warreni Ewer, 1953 is also indistinguishable from *T. ralphi* or *E. crocea* and Watson (1980) formally synonymized it with *E. ralphi*. Material from South Africa examined for this study was indistinguishable from American or European *E. crocea* and also had identical 16S sequences (Fig. 1). The occurrence of typical *E. crocea* in New Zealand (Schuchert 1996) further supports the conclusion that *T. ralphi* is probably not a southern form of *E. crocea*.

Millard (1975) regarded *Tubularia sertularellae* Stechow, 1923a as questionably conspecific with *T. warreni*. *Tubularia sertularellae* must, however, be regarded as indeterminate because it was based on juvenile, non-reproductive animals. Its occurrence in 100 m depth and on a *Sertularella* species would be very unusual for *E. crocea* and they are certainly separate species.

Hirohito (1988) regarded *Tubularia sagamina* Stechow, 1908a as conspecific with *T. mesembryanthemum*, a nominal species here referred to *E. crocea*. Although Stechow (1923a) described *T. sagamina* as reaching up to 16 cm and having up to 50 tentacles, which is quite outside the observed variability of *E. crocea*, it is here included as a questionable synonym of *E. crocea*.

Franzen & Hündgen (1986) reported upon the ultrastructure of a hydroid they identified as *Tubularia mesembryanthemum*. They apparently never observed gonophores. Their figures show a small *Ectopleura* species with capitate oral tentacles. This, as well as its original substrate and the fact that it could easily be cultivated, make it quite certain that they had in fact *Ectopleura wrighti* Petersen, 1979.

REMARKS: The 6-8 crests on the female sporosacs are diagnostic of this species. Unfortunately, they can sometimes be absent. A female colony from the Mediterranean (MHNG INVE 25959) apparently lacked such crests and was therefore identified by myself as *E. larynx* (Schuchert 2001a: fig. 30d). Because the hydranths were larger than usual for *E. larynx* and the sporosacs contained more than one actinula it was thoroughly re-examined. This revealed that a few sporosacs have nevertheless eight indistinct crests and it must therefore belong to *T. crocea*.

Ectopleura wrighti Petersen, 1979 Fig. 7

Acharadria larynx Wright, 1863a: 378, pl. 17 figs 7-8. – Wright, 1863b: 50, pl. 5 figs 7-8. – Hincks, 1868: 134, pl. 23 fig 3. – Allman, 1872: 376, fig. 8. – Stechow, 1923b: 48.
Vorticlava proteus Wright, 1863a: 439, pl. 17 figs 1-6. – Wright, 1863b: 50, pl. 5 fig. 1-6. – Hincks, 1868: 133, pl. 23, fig. 2.
Ectopleura dumortieri. – Graeffe, 1884: 254. – Neppi & Stiasny, 1913: 14, pl. 1 fig. 7. [not *Ectopleura dumortieri* (van Beneden, 1844)]
Ectopleura larynx. – Brinckmann-Voss, 1970: 25, text-figs 26-28. [not *Ectopleura larynx* (Ellis & Solander, 1786)]
Ectopleura wrighti Petersen, 1979: 121, fig 12. – Petersen, 1990: 164, fig. 21A-B. – Peña Cantero & García Carrascosa, 2002: 43, fig. 9a-b. – Bouillon *et al*., 2004: 106, fig. 56E.
in part *Ectopleura dumortieri*. – Goy, 1973: 972 [1 specimen with two tentacles].
Tubularia mesembryanthemum. – Franzen & Hündgen, 1986: 401, figs 1-32. [not *Tubularia mesembryanthemum* Allman, 1872 = *E. crocea*]
Ectopleura minerva. – Goy *et al*., 1991: 104, fig 8. [not *Ectopleura minerva* Mayer, 1900]

MATERIAL EXAMINED: BMNH 1899.5.1.139, as *Acharadria*; English Channel, Herm Island; Hincks collection, on piece of dead shell, young gonophores present. – Mediterranean, Banylus-sur-Mer; polyp stage collected 13.12.1991; on calcareous concretions; not preserved. – Mediterranean, Spain, Mallorca; polyp stage collected 16.06.1997; on sponge; not preserved. – MHNG INVE 27331; Mediterranean, Spain, Mallorca; collected 26.08.1999; had medusa buds when collected, colony cultivated, medusae released and reared until beginning of gonad maturation; 16S sequence **FN687541**. – MHNG INVE 54078; Atlantic, Spain, Basque Country, San Sebastián; collected August 2006 by A. Altuna; on *Cystoseira tamariscifolia*; 16S sequence identical to **FN687541**.

DIAGNOSIS: Tubulariidae producing free medusae, medusae when released and when mature with only two opposite two tentacles. Hydroid stage small, with somewhat capitate oral tentacles.

DESCRIPTION (Brinckmann-Voss, 1970; own data): Hydroid relatively small, forming small colonies comprising only one to four stems. Stolons creeping, but not adhering tightly, branched. Stems arising upright from stolons, more or less isodiametric, rarely branched once, perisarc thin, mostly smooth, thicker part ending at some distance below hydranth and turning into filmy, transparent cover, thus delimiting a neck region. Origin of filmy perisarc below upper end of neck region, forming a more or less distinct perisarc-free part of the neck (collar, Fig. 7B). Hydranth flask-shaped, region above aboral tentacles elongate, with one whorl of 4-10 oral tentacles and one whorl of 8-16 aboral tentacles. Oral tentacles short, held upright, slightly capitate, sometimes with additional swelling below terminal one hence moniliform. Aboral tentacles long and fine, filiform, sometimes with slight, transient terminal swelling, nematocysts concentrated on lower side. Gonophores develop immediately distal to aboral whorl of tentacles on up to eight short blastostyles, arranged in one circle, blastostyle branched or not. Gonophores released as free medusae. Nematocysts of

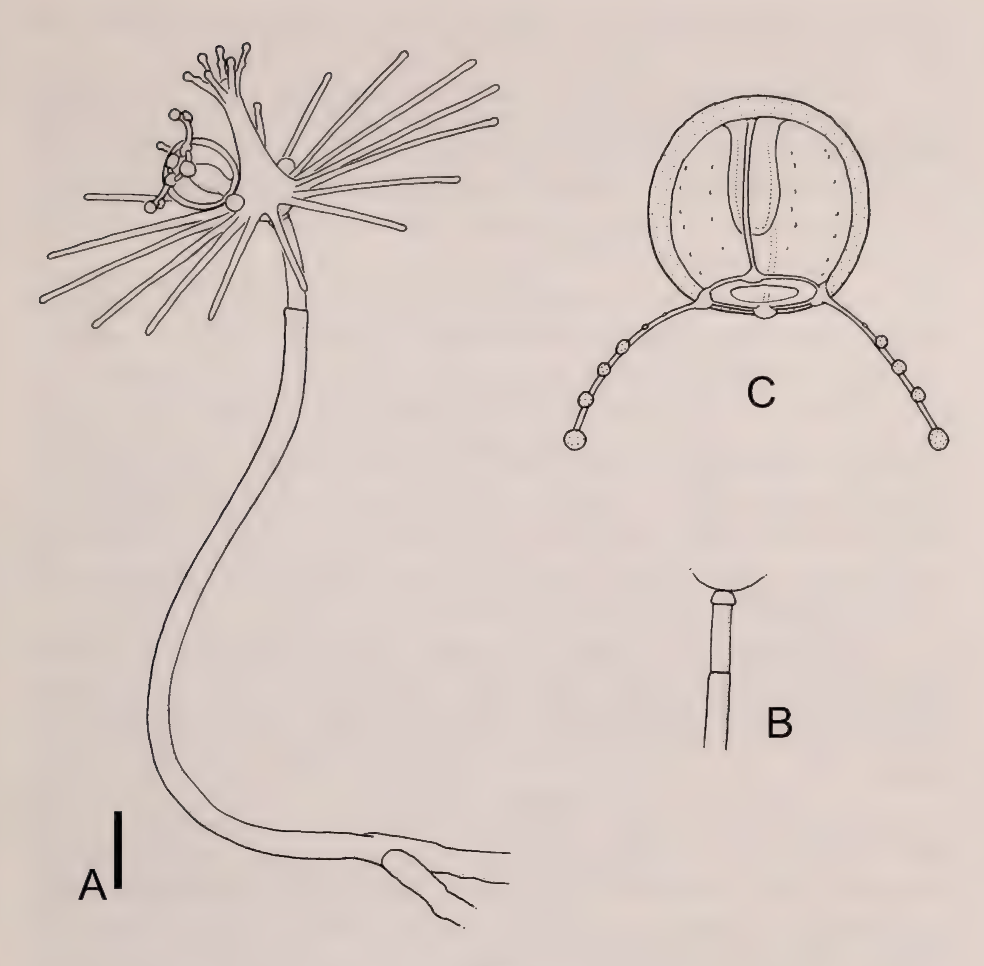


FIG. 7

Ectopleura wrighti Petersen, 1979; after living material from Mallorca. (A) Hydranth with medusa buds, scale bar 1 mm. (B) Neck region of polyp, same scale as A. (C) Medusa about seven days old, bell size about 0.8 mm.

polyp: stenoteles of different size classes, desmonemes, almond-shaped microbasic mastigophores, discharged shaft sometimes slightly swollen and then approaching eurytele condition. Colours: whitish to colourless, transparent.

Nematocysts: stenoteles, desmonemes, and mastigophores.

Newly released medusa spherical, exumbrella with eight meridional lines of stenoteles. With four radial canals and four equal bulbs of which only one opposite pair bears short tentacles, tentacles with one spherical terminal and one subterminal clasping nematocyst cluster. Manubrium short, tubular, spanning ½ of bell cavity, gonads not developed. Colourless.

Mature medusa similar to young medusa, but about two times larger, meridional exumbrellar nematocyst tracks can be partially lost, with only two opposite tentacles,

in addition to terminal nematocyst cluster 2-3 clasping nematocyst clusters on the abaxial side of the tentacles. Manubrium tubular, gonads encircle manubrium.

DIMENSIONS: Height of stems up to 2 cm, usually less than 1 cm, diameter 0.1-0.15 mm. Hydranth when mature and fully expanded about 2 mm high (base to oral tentacles), diameter of tentacle crown when fully expanded up to 6 mm. Bell diameter of newly released medusa 0.5 mm (own observations), or 1 mm (Brinckmann-Voss, 1970). Nematocysts of polyp: stenoteles (6.5-9)x(5-6)μm, desmonemes (5)x (3.5-4)μm, mastigophores (8.5-10)x(4)μm.

OTHER DATA: For the microscopic anatomy and ultrastructure see Franzen & Hündgen (1986, as *Tubularia mesembryanthemum*, misidentification).

BIOLOGY: The polyp occurs in depths of 0.5-40 m in the rocky littoral on a variety of hard substrata (shells, spines of *Stylocidaris*, *Posidonia oceanica* roots, *Microcosmos* spec., rock, concretions, algae, *Eudendrium* spec., barnacles: Motz-Kossowska, 1905; Brinckmann-Voss 1970; Boero & Fresi, 1986; own data). In the Mediterranean, the polyp can perhaps be found throughout the year, while medusa budding is known to occur from June to August. The polyps can easily be maintained in culture, even in rather small containers. They adapt their size to the available water level. In contradistinction, the medusa is very difficult to rear.

DISTRIBUTION: Mediterranean to southern England. In the Atlantic recorded from the Bay of Biscay (this study), Madeira (Brinckmann-Voss, 1970), Brittany (Teissier, 1950, but see Teissier (1965), referred to *E. dumortieri*), English Channel (Allman, 1872), the Celtic Sea (Wright, 1963b). Type locality: Ilfracombe, Devon, England.

REMARKS: The description of *Acharadria larynx* by Wright (1863a, b) was rather short and based on infertile material, but the figures clearly show the capitate oral tentacles. There exists likely no type material. Petersen (1990) thought that it could also pertain to a young *E. larynx* and he therefore expressed some doubts on the presence of this species in the British Isles and that *E. wrighti* might be a Mediterranean species. The species does however also occur in the Atlantic, although it is clearly more common in the Mediterranean (see above). The medusa has only very rarely been reported, likely due to its small size and lack of distinctive features.

The Mediterranean records of *Ectopleura minerva* Mayer, 1900 described by Goy (1973) and Goy *et al.* (1991) are based on two individuals only. The specimen described and depicted in Goy *et al.* (1991) was smaller than normal for *E. minerva* (1 mm versus 2.5 mm as given in Mayer, 1910) and it lacked the apical projection. It matches much more *E. wrighti* as given by Brinckmann-Voss (1970) and as described above. The Mediterranean records of *E. minerva* are thus most probably attributable *E. wrighti*. There are no other European records of *E. minerva* and it must therefore be considered absent from the ERMS zone. Identifying *E. minerva* medusae outside the region from where the species was originally described (Florida) is actually almost impossible and should be avoided. Several nominal *Ectopleura* species with two tentacled-medusae are known (see also Petersen, 1990: 167; Schuchert, 2003: 479), and the status of most of them is unclear (Schuchert, 1996). The complete life-cycle is

only known of *E. wrighti*, *E. minerva* and others known from the medusa stage only, while *E. viridis* (Pictet, 1893), *E. pacifica* (Thornely, 1900) and *E. mayeri* Petersen, 1990 are only known as polyp stages. All these *Ectopleura* medusae are quite simple and species distinction should rather rely on the more complex polyp stage. The life cycles of *E. minerva*, *E. viridis*, *E. pacifica*, and *E. mayeri* must be known before any of these nominal species can be identified outside the region of their respective type localities.

Ectopleura dumortierii (van Beneden, 1844) Fig. 8

Tubularia Dumortierii van Beneden, 1844a: 50, pl. 2.

Tubularia dumortieri. – Johnston, 1847: 50, pl. 7 figs 1-2. – Hincks, 1868: 124, pl. 21 fig. 4. – Allman, 1872: 424. – Haeckel, 1879: 22. – Böhm, 1879: 198, pl. 7 figs 10-13. – Hartlaub, 1907: 94, figs 90-91. – Mayer, 1910: 69, pl. 5, figs 4-5, pl. 6 figs 1,1', 2. – Vervoort, 1946: 107, fig 42. [incorrect spelling]

Tubularia costata McCrady, 1859: 156. – Calder, 1975: 293, synonym.

Ectopleura ochracea L. Agassiz, 1862: 343. – Agassiz, 1865: 191, figs 320-323. – Mayer, 1910: 69, synonym.

Not *Ectopleura dumortieri*. – Graeffe, 1884: 354. – Neppi & Stiasny, 1913: 14, pl. 1 fig. 7. [= *E. wrighti*]

Ectopleura prolifica Hargitt, 1908: 106, figs 8-11.

Ectopleura dumortieri. – Weill, 1934: 373, figs 221-222. – Fraser, 1944: 92, pl. 15 fig. 65. – Russell, 1953: 76, fig. 33A-C, pl. 3 figs 5-6. – Werner & Aurich, 1955: 236, figs 1-8. – Aurich, 1958: 207, figs. 1-6. – Kramp, 1959: 88, fig. 37. – Kramp, 1961: 34. – Kühl, 1962: 215, fig. 5. – Kramp, 1968: 13, fig. 23. – Brinckmann-Voss, 1970: 22, text-figs 22-25, pl. 2 fig. 1. – Calder, 1971: 12. – Lagardère & Tardy, 1980: 266, pl. 1a-f. – Boero, 1984: 98. – Hirohito, 1988: 16, fig. 3a-b. – Petersen, 1990: 159, fig. 10A-C, synonymy. – Goy *et al.*, 1991: 103, fig 7. – Bouillon *et al.*, 2004: 105, fig. 55G-J. – Galea, 2007: 31, fig. 8A–C, pl. 2A. [incorrect spelling]

Ectopleura octogona Thiel, 1938: 292, fig. 1. – Kramp, 1955: 244, synonym.

? *Ectopleura grandis*. – Spracklin, 1982: 240, fig. 113b. – Wedler & Larson, 1986: 71, misidentification.

? *Ectopleura dumortieri*. – Wedler & Larson, 1986: 71, fig. 1C.

Ectopleura dumortierii. – Migotto, 1996: 24, Brazil.

Material examined: BMNH 1912.12.21.403; Belgium; Ostend; on *Tubularia indivisa*; with medusa buds; collected by Prof. E. van Beneden, ex. Norman collection; this is potentially paratype material. – BMNH 1955.11.23.1879; England; Plymouth; collected 02.10.1934; 1 polyp and 1 medusa, F. S. Russell collection. – BMNH 1989.8.3.1; Brazil; Paranagua Bay, Cotinga; polyps collected 21.08.1987; with medusa buds. – ZMUC, no registration number; USA; Connecticut, Noank; collected 1879; leg. C. Nutting. – ZMUC, no registration number; The Netherlands; Zandvort; collected 19.09.1948; on wood; polyp with medusa buds. – MHNG INVE 48728; Chile; Huinay, Punta Llonca; polyps collected 14.02.2006; with medusa buds; material of Galea (2007). – MHNG INVE 49039; Chile; Huinay, depth 0-50 m; several medusae from plankton collected 12.01-19.02.2006, material of Galea (2007). – France; Brittany, Roscoff, 048.730°N 004.000°W, 10-20 m; medusa collected 05.06.2000; not preserved. – France; Brittany, Roscoff, end of pier of Ferry to Île de Batz, depth 0 m; 1 fertile medusa collected 14.09.2004; not preserved. – France, Normandy, Luc-sur-Mer; depth 0 m; 4 infertile medusae collected 17.08.2005; not preserved; 16S **FN687542**. – England; Plymouth, depth 0-5 m; 26.06.2007; one male medusa; not preserved; 16S sequence **FN687543**. – Colour photograph of living hydranth with medusa buds, originating from The Netherlands, kindly provided by Dr M. Faasse.

Diagnosis: *Ectopleura* species with solitary polyps, stolons simple, unbranched. Producing free medusae, with four tentacles when released from polyp and when mature.

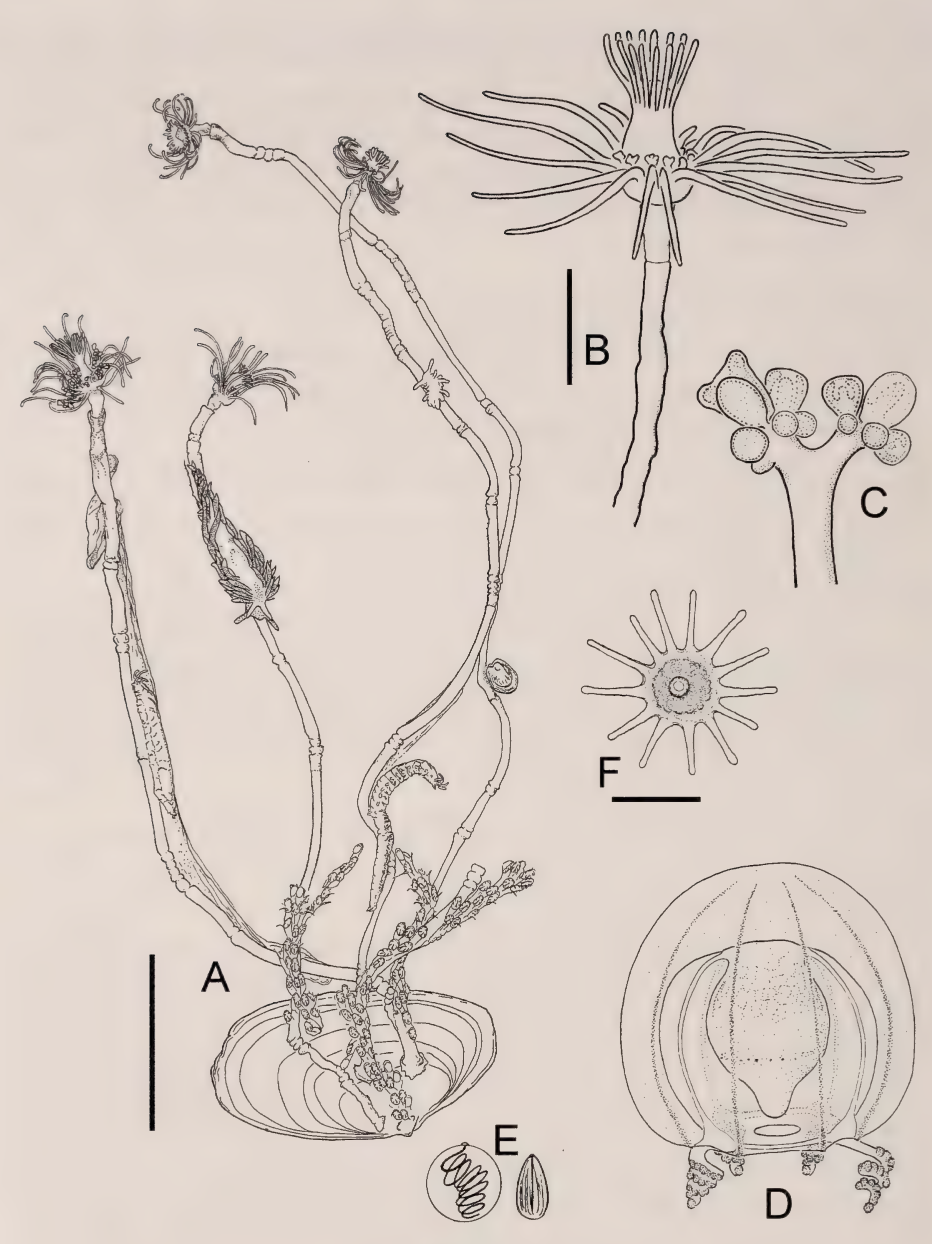


FIG. 8

Ectopleura dumortierii (van Beneden, 1844). (A) Several individual polyps and associated epifauna (bryozoans, polychaetes, opistobranchs), scale bar 5 mm, simplified after Lagardère & Tardy (1980). (B) Hydranth with developing blastostyles, scale bar 2 mm, after preserved material from Plymouth. (C) Short, bifurcated blastostyle with medusa buds; redrawn from van Beneden (1844a). (D) Medusa from plankton, diameter of umbrella 1.9 mm, redrawn and modified after Russell (1953). (E) Spherical anisorhiza and microbasic mastigophore capsules of the medusa; from Weill (1934). (F) Typical, star-shaped actinula, oral view, from Werner & Aurich (1955).

DESCRIPTION (Russell, 1953; Petersen, 1990; own data): Hydroid solitary, occurring singly or in groups of few individuals due to gregarious settling of larvae. Hydrocaulus varying in length depending on environmental factors, either almost isodiametric or diameter increasing up to two times in width from basal to distal end, arising from a simple, unbranched, creeping stolon. Stolon slightly wider than lower part of hydrocaulus, set off from hydrocaulus by constriction of thickened perisarc. When settling on stems of siblings, stolons absent, feigning branched stems. Perisarc of stolon irregularly wavy, annulated at intervals with two to five annulations separated by smooth periderm. Lumen of coenosarc in hydrocaulus with up to four longitudinal ridges. Between stem and hydranth a soft neck-region which is about as high as the hydranth itself, filmy perisarc covering this region very thin, tightly adhering to neck and not loose, origin of filmy perisarc and collar indistinct. Hydranth vasiform, one oral whorl of 15-25 round, filiform tentacles with oval bases which are somewhat adnate to hypostome; one aboral whorl of 20-30 filiform tentacles on which nematocysts are concentrated on aboral side. Medusa buds carried on 8-12 blastostyles, blastostyles initially short and Y-shaped, later longer and with several short side-branches, buds of all developmental stages in dense clusters at ends of side-branches and on main trunk of blastostyle. Eight longitudinal nematocyst tracks visible on advanced buds, arising in pairs from four equally developed marginal bulbs.

Colours: perisarc may be yellowish, blastostyles conspicuously red, hydranth body pink.

Newly liberated medusa similar to mature one, only smaller, with four short tentacles with small terminal knobs and sometimes also one indistinct abaxial nematocyst cluster, fine umbilical canal present or not, no gonads present.

Mature medusa with nearly spherical umbrella, jelly relatively thick, thicker in apical region; velum fairly wide. Very short gastric peduncle usually present. Exumbrella with four pairs of meridional nematocyst bands (stenoteles) of variable length, originating on lateral sides of tentacle bulbs, either terminating at level of stomach base, or nearly uniting at apex of bell. Manubrium fusiform, broadest in middle, shorter or about as long as subumbrellar cavity; extensile, with large parenchymatic cells in upper half of stomach; mouth rim studded with nematocysts. Transverse band of pigment around centre of stomach. Spherical oil droplet near manubrium base in well nourished individuals. Gonads encircle manubrium without subdivision. Females produce only one or more usually two large, opposite eggs at one time. Four radial canals and ring canal thin, inconspicuous. Four marginal bulbs, gastrodermal part large, broad, epidermal part rather small. Four perradial tentacles, each with terminal nematocyst knob and 15-35 abaxial, round nematocyst clusters; tentacles very extensile, but often carried rolled up into a thick short spiral.

Nematocysts (Weill, 1934): stenoteles, desmonemes, spherical heterotrichous anisorhizas, microbasic mastigophores.

Colours of tentacle bulbs brownish or yellow, mouth orange or crimson, with band of fine red spots around centre of stomach, and brownish or yellow circle of pigment around base of stomach near junction of radial canals.

DIMENSIONS: Hydrocaulus 10-100 mm high in mature polyps, hydranth diameter at level of aboral tentacles 1-2 mm, height up to 2 mm, stem diameter normally

about 0.5 mm. Newly liberated medusa 1 mm, mature 1-2 mm, maximally 4 mm high. Later in the year when food gets scarce, the medusae may remain very small (0.25-0.75 mm, Aurich, 1958). Nematocysts of medusa (Weill, 1934): stenoteles 8-12 μm long; desmonemes length 6 μm; anisorhizas diameter 10 μm; mastigophores length 8 μm. Eggs 0.31-0.33 mm (Werner & Aurich, 1955).

Other data: For the nematocysts of the polyp stage see Galea (2007), although this Chilean material may pertain to a very similar, but distinct species. The embryonic development results in a characteristic, star-shaped actinula with 10-13 radiating tentacles held in one plane. The development is rapid, the larvae settle after 4-5 days (Werner & Aurich, 1955). The embryonic development has been described by several authors: Werner & Aurich (1955), Aurich (1955), Kühl & Kühl (1967), and Bodo (1969). Van Beneden (1844a) depicted the development of the medusa buds.

Biology: The polyp occurs along the Atlantic coast usually in depths from 3 to 65 m (Fey, 1970; Lagardère & Tardy, 1980). They are generally rare, but may be abundant locally. They grow on empty shells, other hydroids, stones, and bryozoans. Bottom types are medium to fine sands (Lagardère & Tardy, 1980), stony or coarse gravel grounds (Teissier, 1965; Aurich, 1958), or rock and artificial hard substrata (Fey, 1970). The polyps can form a characteristic facies comprising specific nudibranchs, a tube dwelling polychaete, and bryozoans (Lagardère & Tardy, 1980), see Fig. 8A. The hydroid is eaten by the nudibranchs. Calder (1971) found the polyp also in waters with reduced salinity.

The medusae are found in the surface plankton, usually in low numbers, but they can attain temporarily very high concentrations in the North Sea (up to 4000 per cubic metre; Aurich, 1958). The seasonality in the southern North Sea is June to December, with a maximum in July to September (Hartlaub, 1907; Aurich, 1958). In the English Channel, they occur from May to November (Russell, 1953; Teissier, 1965), in Ireland from May-September (Ballard & Myers, 2000), and the east coast of the USA in the autumn (Calder, 1971). In the Atlantic, the medusa is thus a summer species. This is in contrast with the Mediterranean, where it is present during the winter months, although always in low numbers (Brinckmann-Voss, 1970; 1987).

The medusae are gonochoristic and oviparous (Aurich, 1958). They flee the light (Brinckmann-Voss, 1970).

Distribution: The medusae and the polyps occur along the European Atlantic coast from as far north as Scotland and the North Sea, down south to Portugal (Hartlaub, 1907; Da Cunha, 1944; Russell, 1953, 1957; Aurich, 1958; Teissier, 1965: Allwein, 1968; Fey, 1970; Fraser, 1974; Medel & López-González, 1996; Faasse, 2003). In the western Atlantic they are known from Cape Cod to South Carolina (Calder, 1971; Petersen, 1990). The medusa is also known to occur occasionally in the western and eastern Mediterranean (Brinckmann-Voss, 1970; Goy *et al.*, 1991), but the polyp has apparently only been found once near Naples (Stechow, 1923b). The species has also been reported from the tropical Atlantic, the Indian Ocean, and the Pacific Ocean, but these records likely belong to other species (Petersen, 1990). Type locality: North Sea, Belgium, Ostend.

Remarks: Petersen (1990) reviewed all *Ectopleura* species known from the polyp stage and he also described several new species. There are thus several nominal

species occurring outside the ERMS zone that closely resemble *E. dumortierii*, differing in details of the stolons and the growth form. Petersen thus concludes that records of *E. dumortierii* other than from the North Atlantic and Mediterranean likely pertain to other species. The material from Chile, described in detail by Galea (2007), appears indistinguishable from European *E. dumortierii*, but preliminary 16S data (unpublished) indicate that it is distinct from the European *E. dumortierii*.

Ectopleura sacculifera Kramp, 1957 Fig. 9

Ectopleura sacculifera Kramp, 1957: 7, pl. 2 figs 1-3. – Kramp, 1968: 14, fig. 25. – Brinckmann-Voss, 1970: 27, fig. 29, pl. 2 fig. 2. – Bouillon, 1978b: 280, fig. 17. – Bouillon *et al.*, 2004: 106, fig. 56D.

DIAGNOSIS: *Ectopleura* medusa with two opposite tentacles when mature, manubrium with four perradial pouches covered by gonad tissue.

DESCRIPTION (after Kramp, 1957, Brinckmann-Voss, 1970; Bouillon 1978b): Medusa with oval to spherical umbrella, jelly moderately thick, apex somewhat thickened, exumbrella with eight meridional nematocyst tracks issued in pairs from lateral sides of marginal bulbs, tracks on shallow ridges of umbrella, these ridges get much accentuated in preserved animals. Manubrium half as long as bell cavity, tubular, with four perradial sac-like pouches in middle, gonads cover manubrium wall and pouches. Four radial canals and circular canal present. Four marginal bulbs, one opposite pair somewhat larger and only this pair bearing the two tentacles. Tentacles long, ending in terminal, spherical nematocyst cluster, distal region of tentacles with abaxial clasping nematocyst buttons, up to 25 in Pacific animals, up to 7 in Mediterranean medusae.

Nematocysts: two types of stenoteles, spherical basitrichous isorhizas, desmonemes, oval microbasic euryteles.

Polyp stage unknown.

DIMENSIONS: Umbrella height 3 mm. For nematocysts dimensions see Bouillon (1978b).

DISTRIBUTION: Pacific Ocean off Ecuador, Papua New Guinea, Indian Ocean, Western Mediterranean (Bouillon, 1978b). Type locality: Pacific coast of Ecuador, 002.872°S 082.325°W, 0-100 m.

REMARKS: *Ectopleura sacculifera* in the Mediterranean is known only from a single specimen collected near Naples (Brinckmann-Voss, 1970). It is better known in the Indo-Pacific.

Genus ***Hybocodon*** L. Agassiz, 1860

Diplonema Greene, 1857; type species *Diplonema islandica* Greene, 1857 [syn. *Hybocodon prolifer*], homonym of *Diplonema* Loew, 1845 [Diptera, Insecta] and *Diplonema* Griessmann [Eugleniidae, Protozoa].

Hybocodon L. Agassiz, 1860; type species *Hybocodon prolifer* L. Agassiz, 1860 by monotypy.

Diplura Allman, 1864b; invalid junior homonym of *Diplura* Koch [Araneae].

Hypocodon Müller, 1870. [incorrect spelling]

Amphicodon Haeckel, 1879, no type species designated.

Auliscus Saemundsson, 1899, type species *Auliscus pulcher* Saemundsson, 1899 [syn. *Hybocodon prolifer*].

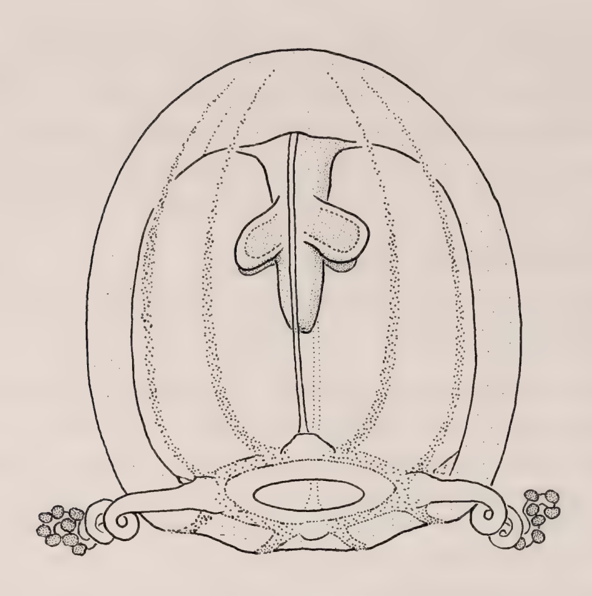


FIG. 9

Ectopleura sacculifera Kramp, 1957. Mediterranean medusa after life, bell size about 1 mm; redrawn and modified after Brinckmann-Voss (1970).

DIAGNOSIS: Solitary tubulariid hydroids with long, perisarc-covered caulus and a neck region below hydranth. Hydrorhiza irregularly branched, slightly swollen and usually embedded in sponges. Perisarc thin, loose around neck region, secreted from groove between hydranth and neck. Hydrocaulus tubular, soft tissue with central lumen, with up to 14 longitudinal ridges projecting into lumen. Hydranth vasiform, with two closely set whorls of oral tentacles and one whorl of aboral tentacles. Gonophores arise from branching blastostyles distal to aboral whorl of tentacles, released as free medusae.

Medusa with bilaterally symmetrical umbrella and oblique margin. Exumbrella with or without five meridional nematocyst tracks. Manubrium cylindrical, on short peduncle, not extending beyond umbrella margin. With one shorter, two medium sized and one longer radial canals. One broad, bean-shaped marginal bulb with long, moniliform tentacle at end of longest radial canal, other three perradial bulbs small, equally developed.

REMARKS: There is only one species of *Hybocodon* in the ERMS zone.

Hybocodon prolifer L. Agassiz, 1860 Fig. 10

Coryne fritillaria Steenstrup, 1842a-b: 20, pl. 1 figs 44-46, medusa only, hydroid likely *S. lovenii* (M. Sars, 1846).

? *Diplonema islandica* Greene, 1857: 247, pl. 15 fig 7a.

? *Steenstrupia oweni* Greene, 1857: 248. pl. 15 fig. 8a.

? *Steentrupia globosa* Sars, 1860a: 101. – Sars, 1877: 20, pl. 1 figs 1-6.

Hybocodon prolifer L. Agassiz, 1860: 45, figs 11-14. – L. Agassiz, 1862: 243, pl. 23a figs 10-11, pl. 25 fig. 19. – Nutting, 1901: 341, fig. 76. – Hartlaub, 1907: 96, figs 92-93.– Mayer, 1910: 38, fig. 10, pl. 2 fig. 1, pl. 3 fig. 3. – Kramp, 1926: 33, figs 29-34, pl. 1 fig.

9, chart VI. – Hargitt, 1927: 498. – Uchida, 1927: 192, fig. 29. – Fraser, 1937: 54, pl. 2 fig. 46. – Fraser, 1944: 106, pl. 18 fig. 78. – Vervoort, 1946: 109, fig 43. – Russell, 1953: 79, fig. 34, pl. 3 figs 3-4. – Aurich, 1958: 216. – Kramp, 1959: 86, fig. 33. – Kramp, 1961: 43. – Kramp, 1968: 12, fig. 19. – Russell, 1970: 233. – Arai & Brinckmann-Voss, 1980: 10, fig. 4. – Petersen, 1990: 192, fig. 37. – Schuchert, 2001a: 44. – Bouillon *et al.*, 2004: 107, fig. 56F-H.

Diplura fritillaria. – Allman, 1872: 320.

Amphicodon globosus Haeckel, 1879: 36. – Kramp, 1926: 33, synonym.

Amphicodon amphipleurus Haeckel, 1879: 36. – Kramp, 1926: 33, synonym.

Amphicodon fritillaria. – Browne, 1895: 251.

Tubularia prolifera. – Bonnevie, 1899: 28, pl. 1 fig. 6.

Auliscus pulcher Saemundsson, 1899: 425, pl. 4. – Petersen, 1990: 193, synonym.

Hybocodon pulcher. – Hartlaub, 1907: 98, figs 94-97.

Hybocodon christinae Hartlaub, 1907: 102, fig. 98. – Kramp, 1959: 86, synyonym.

? *Amphicodon gravidum* Linko, 1905: 215.

Tubularia pulcher. – Broch, 1916: 22, pl. 2 fig. 16.

Tubularia prolifer. – Naumov, 1969: 233, figs 102-105.

Tubularia christinae. – Naumov, 1969: 236, fig. 106.

not *H. chilensis* Hartlaub, 1905: 545, figs V-W. – Galea, 2006: 57, figs 1-4.

not *Hybocodon prolifer*. – Ralph, 1953: 70, figs 11 & 22. – Bouillon, 1995: 224. – Schuchert, 1996: 113, fig. 68a-e. [all *H. chilensis*, see Galea, 2006]

Material examined: BMNH 1985.9.1.11; England, Plymouth; 2 polyps, collected by W. J. Rees 07.03.1938; stems embedded in sponge. – Scotland, Dunstaffnage Bay; surface plankton collected 10-13 May 2004, about 10 medusae in good condition, some with gonads, examined alive, material used for DNA extraction, 16S sequence accession number **FN687544**. – France, Brittany, Roscoff; one medusa from plankton collected 31.03.1998; not preserved, material used for DNA extraction; 400 bp of 16S gene identical to **FN687544**.

Diagnosis: As for genus *Hybocodon*, medusa with five meridional nematocyst tracks on exumbrella, budding secondary medusae from the single tentacular bulb.

Description (Russell, 1953; Petersen, 1990; own data): Hydroid associated with sponges, solitary, occurring singly or in groups of 2-4 individuals, likely due to gregarious settling of larvae. Stem base and hydrorhiza embedded in sponge, with neck region between stem and hydranth, stem straight, perisarc smooth, slightly wrinkled basally, stem widening from thin base towards distal end, irregularly bent basally, perisarc strongly developed around transition between hydrocaulus and hydrorhiza; usually one hydrorhizal process (stolon) and one or two thinner supporting tubes developed from basalmost part of hydrocaulaus. Central lumen of stem with up to 14 ridges distally, merging into four ridges towards base, ridges visible from outside as striation. Neck region bulb-shaped, about as high as the hydranth itself, covered by loose, funnel-like, membranous perisarc originating from groove between neck and hydranth.

Hydranth vasiform, with about 30-35 short oral tentacles in two alternating whorls, and 25-30 long aboral tentacles. Oral tentacles adnate to hypostome, with concentration of nematocysts on tips and distal part of aboral surface, tentacles of outer whorl longer than those of inner circlet; bases of oral and aboral tentacles continued as ridges on hydranth; cross-section of aboral tentacles near base oval. Medusa buds carried in clusters on eight to twelve short, dichotomously branched blastostyles; medusa buds with five meridional nematocyst tracks and one larger tentacle bud which already carries additional developing medusae in older buds. Colours (Agassiz, 1862): deep orange-red.

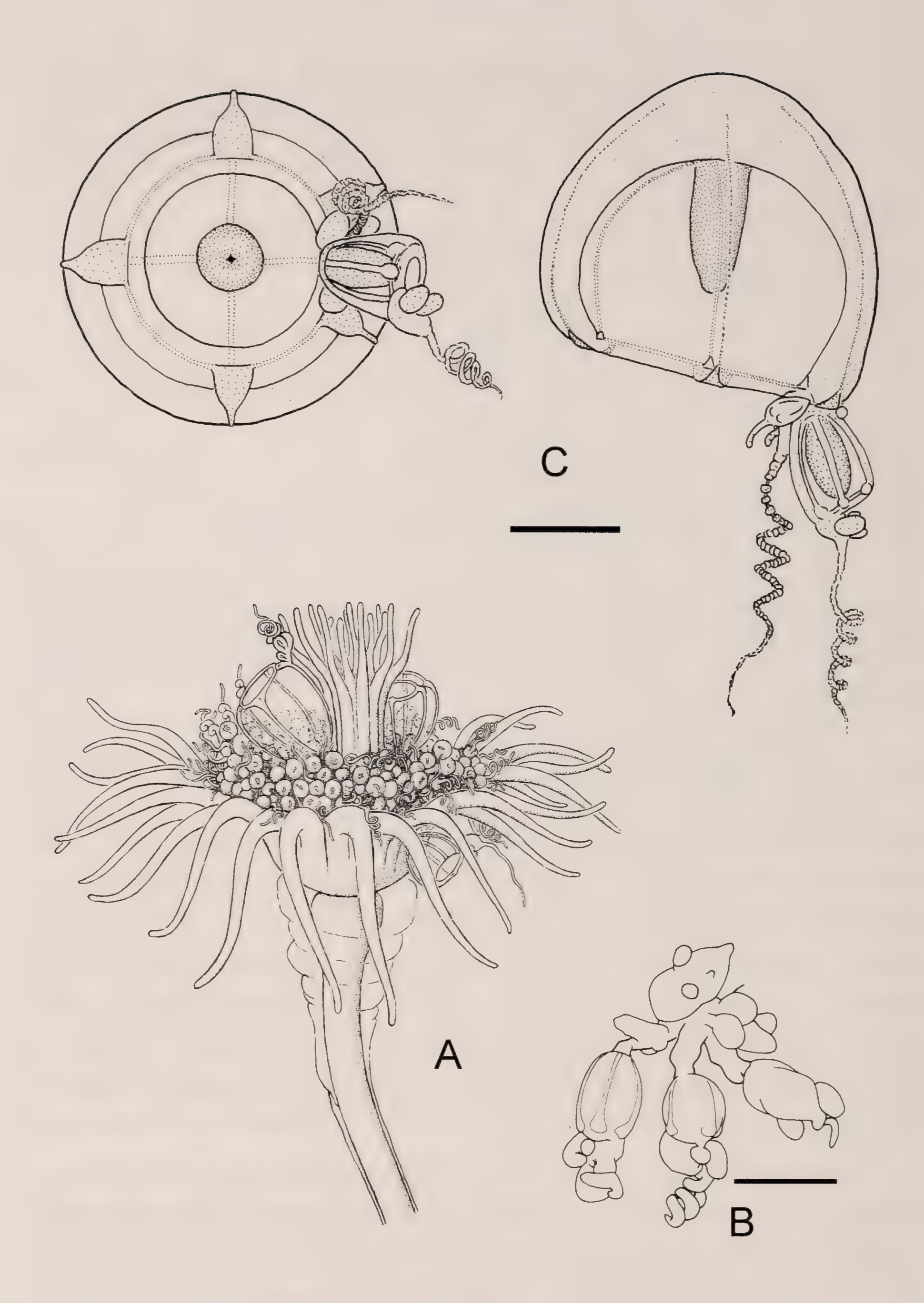


FIG. 10

Hybocodon prolifer L. Agassiz, 1860. (A) Hydranth with numerous medusa buds, modified after Agassiz (1862) and Mayer (1910). (B) Blastostyles with medusa buds; scale bar 0.5 mm, from Petersen (1990). (C) Medusa with secondary medusae, left in oral view, right in side-view, drawn after life; scale bar 1 mm.

Newly released medusa very similar to fully grown ones but smaller, tentacles relatively well developed, with umbilical canal, usually disappearing soon, but may persist into adulthood. Newly budded medusae already bear secondary buds which in turn may already have tertiary buds.

Mature medusa with bell-shaped umbrella, higher than wide with rounded summit; umbrella margin oblique to vertical axis sloping from tentacular side; without apical process; jelly thick, especially on tentacular side and on top, sometimes short gastric peduncle present. Exumbrella with five meridional lines of nematocysts, three issuing from atentacular bulbs and another two laterally from broad tentacular bulb. Stomach fusiform, about half to two thirds the length of umbrella cavity, never reaching beyond margin in full extension. Mouth simple, surrounded by narrow ring of nematocysts. Gonads completely surrounding stomach, leaving top part and mouth free. Animals gonochoristic, females with 1-4 amoeboid eggs, developing into young polyps in umbrellar cavity, animals thus viviparous. Four radial canals and ring canal fairly broad; radial canal on tentacular side longer than the one opposite it, may also be thicker. Only one marginal bulb bearing a tentacle, broad, bipartite, three other bulbs much smaller, rudimentary. Medusa buds developed from tentacular bulb and giving it sometimes a compound appearance with up to four tentacles as tentacles of buds develop rather rapidly and in advance of rest of medusa. Budding usually stops with the maturation of the gonads, but exceptions are known. Tentacles moniliform with up to 50 clasping or ring-like nematocyst clusters.

Colours: bulbs, mouth and upper end of stomach bright red or reddish brown; stomach pale yellow; gastrodermis of marginal tentacles and subumbrella pink; exumbrellar nematocyst tracks pink.

Dimensions: Polyps 1-5 cm high, stem diameter basally 1 mm, extended aboral tentacles up to 5 mm long. Newly liberated medusa 1 mm (primary medusae). Fully grown medusa 2-4 mm high. Egg size 0.3-0.5 mm (Aurich, 1958).

Other data: Agassiz (1862) described the hydroid as devoid of blastostyles, but this was an error corrected by Hargitt (1927). Aurich (1958) observed an oil droplet at base of manubrium in well nourished medusae. Some aspects of the microanatomy and histology of the medusa are presented by Kramp (1926). Uchida (1927) reported abnormal specimens with eight radial canals. For the development of the germ cells and embryonic development see Browne (1895), Müller (1908), Hargitt (1917), and Aurich (1958). The nematocysts are not known. For closely related species see Millard (1975), Schuchert (1996), and Galea (2006).

Biology: The polyp is a littoral species occurring in shallow depths and even large, protected rock-pools, but has only rarely been found along the European coasts (Reykjavik: Saemundsson, 1899; Plymouth: Russell, 1957). The specimens from Plymouth, several animals were taken over a long time period, were always associated with the sponge *Desmacidon fruticosum* (Montagu). It is not known whether this is an obligatory association. Hydroids releasing medusae were observed in March and April. For the western Atlantic, medusa budding was observed from January to May (Mayer, 1910). In the North Sea, the occurrence of the medusa shows some linkage to rocks and rocky bottoms off the coast (Aurich, 1958). The first medusae appear in March,

densities then increase until June up to 1200 individual per cubic metre; once the temperature reaches 14-16°C, sexual reproduction is initiated (Aurich, 1958). The medusae disappear in July, being occasionally met with as late as August. Usually, sexually active animals do not bud medusae anymore, but exceptions are possible (Russell, 1953).

Distribution: The medusa is widely distributed in the north Atlantic and Pacific, known from Newfoundland to Chesapeake Bay, western and eastern Greenland, Iceland (north and west coast), north-west Europe from the English Channel northwards to Beren Island and the Arctic Sea, also Bering Sea, Sea of Okhotsk, Hokkaido to Kamchatka, Alaska, Puget Sound. The polyp is known from the east coast of North America, Plymouth on the south coast of England, and Iceland (Russell, 1953; Kramp, 1926, 1959; Aurich, 1958; Fraser, 1974; Arai & Brinckmann-Voss, 1980; Petersen, 1990; Schuchert, 2001a). The records of the polyp from northern Spain (Medel & López-González, 1996) are likely misidentifications (A. Altuna, pers. com.). A single medusa has once been found in this region (Moreno & Fernández-Alcazar, 1984). Although the southern limit of its range seems to be the English Channel, some rare specimens may occasionally be transported further south by currents. The Mediterranean records (Medel & López-González, 1996) need a reconfirmation. Type locality: Nahant, north of Boston, USA.

Remarks: It was in 1860 when Agassiz introduced the name *Hybocodon prolifer* and not 1862 as given by many authors. The taxonomic history of this species is complicated and the synonymy given above reflects the views of Browne (1895), Mayer (1910), Kramp (1926), Russell (1953), Arai & Brinckmann-Voss (1980), and Petersen (1990). Most questionable synonyms are based on inadequate descriptions which do not permit a reliable comparison of the species. Some nominal species originally described from the Pacific have not been included in the synonymy as they may pertain to other valid species. Galea (2006) recently reviewed the better known species and concludes that *H. chilensis* Hartlaub, 1905 is likely valid and distinct from *H. prolifer* as the medusa never produces secondary medusae. The medusae of the North Pacific (Uchida, 1927; Arai & Brinckmann-Voss, 1980), however, do produce secondary medusae and are thus likely *H. prolifer*.

Although the medusa is quite common in the British Isles and the North Sea, the hydroid has not been found very often, even though it is a littoral species. This is probably connected with its preference for sheltered, shaded spaces under rocks from where it can only be collected by hand (Petersen, 1990).

Genus ***Bouillonia*** Petersen, 1990

Bouillonia Petersen, 1990; type species *Tubularia cornucopia* Bonnevie, 1898, by original designation.

Diagnosis: Hydroid solitary; hydrocaulus curved, diameter widening six times or more towards distal, base attached by basal disc or short stolons. Centre of hydrocaulus filled by parenchymatic tissue, in periphery a circle of several equally-sized longitudinal canals of oval cross-section. Filmy perisarc covering short neck region secreted from groove on hydranth just under aboral tentacle whorl. Hydranth with rounded base, hypostome wide, cylindrical with wide mouth; several closely set whorls

of short oral filiform tentacles and one whorl of longer aboral tentacles. Gonophores fixed sporosacs on dichotomously branched blastostyles.

REMARKS: Only one species of the genus occurs in the ERMS zone.

Bouillonia cornucopia (Bonnevie, 1898) Fig. 11

Tubularia cornucopia Bonnevie, 1898: 474, pl. 26 fig. 20. – Bonnevie, 1899: 29, pl. 2 figs. 1, 1a-c. – Jäderholm, 1902: 5.
not *Tubularia cornucopia*. – Broch, 1916: 29. [= *Stephanoscyphus simplex*]
? *Bouillonia cornucopia*. – Petersen, 1990: 176, fig. 28.
Bouillonia cornucopia. – Schuchert, 2001a: 42. – Svoboda *et al*., 2006: 192, figs 1, 2a, 8, 13, 16, 17a, 20a, 21a-d, tables 1, 2.
? *Bouillonia* spec. – Svoboda *et al*., 2006: 196, figs 6, 7, 20b-c, 22, 23.

DIAGNOSIS (Svoboda *et al*., 2006): *Bouillonia* species with stem up to 12 cm high, stem diameter widening up to 10 times distally, basal attachment via two creeping stolons, hydranth deep-red with 35-40 oral tentacles in several whorls.

DESCRIPTION AND FIGURES: See Svoboda *et al*. (2006).

DISTRIBUTION: A rare deep-sea tubulariid, occurring in depths of > 2000 m. It is known only from the type-locality: 77.97°N 05.17°E (Spitsbergen area), 2438 m depth and perhaps from the area between Greenland and Jan Mayen (Jäderholm, 1902). Petersen also attributed material from the Norwegian Sea to this species, but Svoboda *et al*. (2006) think that these specimens belong to a distinct species.

REMARKS: Svoboda *et al*. (2006) re-examined and revised all available *Bouillonia* specimens, attributing them to three different morpho-species (two Arctic, one Antarctic). They give a detailed account of the morphology and also of the nematocysts. Svoboda *et al*. (2006) think that Petersen's (1990) material of *B. cornucopia* from the Norwegian Sea belongs to a different species, but they did not name it. The differences of the two purported species are relatively small, taking into account the usually very extensive variation of other tubulariids. Only very few *B. cornucopia* been seen so far, which drastically limits our knowledge of the intraspecific variation. Once more material becomes known, such apparent differences may well disappear, because intermediate forms will link the previously known morphotypes. The main difference between the two morphotypes is that *B. cornucopia* has stolons, while Petersen's material had attachment discs. In other tubulariids, both types of attachment can occur, likely depending on the substrate, e. g. in *T. regalis* or *E. dumortierii*.

Genus ***Zyzzyzus*** Stechow, 1921

Zyzzyzus Stechow, 1921a; type species *Tubularia solitaria* Warren, 1906. [= *Zyzzyzus warreni* Calder, 1988, replacement name for invalid *Tubularia solitaria* Warren, 1906 (see Calder, 1988)]
Zyzzygus Neave, 1940. [incorrect spelling]
Zyzzyzuz Bouillon, 1985a. [incorrect spelling]

DIAGNOSIS: Hydroid solitary; hydrocaulus stout, widening towards base; hydrorhiza forming rootlets and swollen storage tubers. Centre of hydrocaulus filled by parenchymatic tissue, in periphery a circle of several equally-sized longitudinal canals. Between caulus and hydranth long cylindrical neck region covered by thin closely



FIG. 11

Bouillonia cornucopia (Bonnevie, 1898), syntype specimen after drawing of M. Sars, from Bonnevie (1899).

fitting perisarc originating in groove immediately under hydranth. Hydranth with one or more close-set oral whorls of filiform tentacles and one whorl of longer, filiform to pseudofiliform aboral tentacles with laterally flattened bases which are not continued as ridges over hydranth base. Gonophores radially symmetric cryptomedusoids, carried singly on hydranth or on dichotomously branched blastostyles distal to aboral tentacle whorl.

REMARKS: Only one species of the genus occurs in the ERMS zone.

Zyzzyzus robustus Petersen, 1990

Zyzzyzus robustus Petersen, 1990: 183, figs. 32-33. – Schuchert, 2001a: 42 (footnote). – Campos *et al.*, 2007: 10.

DIAGNOSIS: *Zyzzyzus* species lacking a groove at region of secretion of perisarc, with long and monopodial blastostyles, distance between adjacent aboral tentacles inferior to diameter of tentacular base (Campos *et al.*, 2007).

Description and figures: See Petersen (1990) and Campos *et al*. (2007).

Biology: One polyp of type material had fibres on its hydrorhiza, indicating that it was embedded in sponges, others were attached to rocks and encrusting bryozoans, depth range 140 to 225 m (Campos *et al*., 2007).

Distribution: Southern Greenland. Type locality: Greenland, off Akuliaruseq, 60.150°N 44.167°W, 140 m.

Remarks: The species is well described and depicted in Petersen (1990) and Campos *et al*. (2007). As it occurs only at the very limit of the ERMS zone and is not really a European species, there is no need to repeat the descriptions here.

Family Corymorphidae Allman, 1872

Corymorphidae Allman, 1872.
Monocaulidae Allman, 1872.
Amalthaeidae Haeckel, 1879.
Euphysidae Haeckel, 1879.
Steenstrupiini Cockerell, 1911.
Branchiocerianthidae Broch, 1916.
Trichorhizini Cockerell, 1911.
Hypolytidae Fraser, 1943.
Paragoteidae Ralph, 1959.

Diagnosis: Solitary hydroids with two sets of tentacles, oral and aboral ones. Oral tentacles in one whorl and moniliform or capitate, or several close-set whorls of filiform tentacles. Aboral tentacles moniliform or filiform in one to three whorls. Hydrocaulus long, basally pointed or rounded, hollow or more or less filled with parenchymatic gastrodermis. With short papillae or longer filaments composed of epidermis with a core of chordoid gastrodermis terminating in non-ciliated statocysts. Gonophores carried singly or on blastostyles just above the aboral tentacle whorl. Gonophores remain fixed as sporosacs or are liberated as free medusae.

Medusa with umbrella that may or may not have an apical projection, no exumbrellar nematocyst tracks, but sometimes long abaxial spurs of marginal bulbs. Manubrium mostly not extending beyond umbrella margin, tubular to fusiform, mouth simple, circular. Either only one fully developed marginal tentacle, or one fully developed tentacle and three shorter ones differing also in structure. Four radial canals and three to four marginal bulbs present, ocelli lacking.

Remarks: For the taxonomic history and synonymy of the family see Calder (1988). Most life-cycles of the Corymorphidae are still unknown, and many nominal species are known only from their medusa phase. It is therefore not surprising that that there is currently no generally accepted idea of the scope of Corymorphidae and their generic subdivision (Kramp, 1949; Rees, 1957; Brinckmann-Voss, 1970; Millard, 1975; Calder, 1988; Petersen, 1990; Pagès & Bouillon, 1997; Brinckmann-Voss & Arai, 1998; Svoboda & Stepanjants, 2001; Bouillon *et al*., 2006). Only a comprehensive molecular phylogenetic analysis can settle the issue. Here, Petersen's (1990) phylogeny based scope of the family is adopted, although admittedly it is likely also only a provisional one. The generic subdivision also largely follows Petersen (1990), who used only a minimal number of genera and synonymized many names.

Petersen excluded *Paragotoea bathybia* from the Corymorphidae, certainly because his scope of the species was based on the incorrect interpretations of Ralph (1959). Pagès & Bouillon (1997) then revised *P. bathybia* and included it in the family Corymorphidae. With its new, restricted scope *Paragotoea* fits well into the family Corymorphidae sensu Petersen. In fact, it is hardly separable from *Corymorpha* sensu Petersen and *Paragotoea* could be synonymized with *Corymorpha*. The medusa of *P. bathybia* is rather similar to *Corymorpha forbesii* and this argument could be used to unite the genera. However, according to Pagès & Bouillon (1997), the cnidome of *P. bathybia* comprises only stenoteles and is thus rather unique. In contradistinction, the cnidome of corymorphid medusae always includes desmonemes and haplonemes, as well as the constant stenoteles (Bouillon, 1985a). Although they did not use the argument of the cnidome, Brinckmann-Voss & Arai (1998) opposed the idea that *Paragotea* should be included in the Corymorphidae. Bouillon *et al*. (2006) continued to include *Paragotoea* in the Corymorphidae. Any further discussions are futile as long as the polyp stage of *Paragotoea* is unknown. For practical reasons *Paragotoea* is here provisionally included in the family Corymorphidae.

The cnidomes of most Corymorphidae (and Tubulariidae) are not well known and no diagnostic differences have been elaborated so far. While most species have relatively similar cnidomes, in some cases diagnostic differences are present (comp. *C. groenlandica*).

The key below is valid only for genera occurring in the ERMS zone. For genera not occurring in the ERMS zone see Bouillon *et al*. (2006).

KEY TO THE GENERA OF CORYMORPHIDAE OF THE ERMS ZONE

1a	polyp stage unknown or only medusa stage available	6
1b	polyp stage known or gonophore remaining fixed as medusoids or sporosacs	2
2a	hydranth large, distinctly bilaterally symmetric, blastostyles arranged U-like	*Branchiocerianthus*
2b	hydranth with radial symmetry, blastostyles arranged in circle	3
3a	polyps small (< 1.5 mm), interstitial, four aboral tentacles	*Siphonohydra*
3b	polyps larger than 1.5 mm, more than four aboral tentacles	4
4a	oral tentacles capitate, aboral tentacles distinctly moniliform	*Euphysa*
4b	oral tentacles filiform, aboral tentacles filiform or indistinctly moniliform	5
5a	hydranth clearly separated from stem, no papillae below aboral tentacles	*Corymorpha*
5b	hydranth not clearly separated from stem, papillae below aboral tentacles	*Gymnogonos*
6a	juvenile and mature medusa with apical process and apical canal	*Corymorpha*
6b	without apical process or apical canal	7
7a	1 tentacle only, terminating in a large, globular nematocyst knob	*Paragotoea*
7b	1-4 tentacles, moniliform	*Euphysa*

Genus ***Corymorpha*** M. Sars, 1835

Corymorpha M. Sars, 1835; type species *Corymorpha nutans* M. Sars, 1835 by monotypy.
Corimorpha van Beneden, 1844b. [incorrect spelling]

Steenstrupia Forbes, 1846; type species *Steenstrupia rubra* Forbes, 1848 [syn. *C. nutans*], designation by Mayer (1910).
Amalthaea O. Schmidt, 1852; type species *Amalthaea uvifera* O. Schmidt, 1852 by monotypy.
Amathaea Sars, 1857. [incorrect spelling]
Cormorpha Sars, 1860a. [incorrect spelling]
Monocaulos Allman, 1864a.
Monocaulus Allman, 1872; justified emendation of spelling; type species *Monocaulus glacialis* by designation of Allman (1872).
Halatractus Allman, 1872; type species *Corymorpha nana* Alder, 1857a by original designation; invalid homonym of *Halatractus* Gill, 1863 [Pisces].
Rhizonema Clark, 1877; type species *Rhizonema carnea* Clark, 1877 by original designation.
? *Microcampana* Fewkes, 1889; type species *Microcampana conica* Fewkes, 1889 by monotypy.
Lampra Bonnevie, 1898; invalid as pre-occupied by identical genus names of Insecta and Crustacea, see Svoboda & Stepanjants (2001).
? *Tubuletta* Haeckel, 1899; type species *Tubuletta splendida* Haeckel, 1899.
Euphysora Maas, 1905; type species *Euphysora bigelowi* Maas, 1905 after Kramp (1961).
Eucorymorpha Broch, 1910; no type species designated.
? *Gotoea* Uchida, 1927; type species *Gotoea typica* Uchida, 1927 by monotypy.
Vannuccia Brinckmann-Voss, 1967; type species *Hybocodon forbesii* Mayer, 1894, by original designation; name pre-occupied by *Vannuccia* Marcus, 1948 [Plathyhelminthes].
Altairina Vargas Hernandez & Ochoa-Figuera, 1991; type species *Hybocodon forbesii* Mayer, 1894 by original designation.

DIAGNOSIS: Solitary hydroids with more or less vasiform hydranth and long caulus. Hydranth with one or several closely set oral whorls of 16 or more moniliform or filiform tentacles and one aboral whorl of 16 or more long, non-contractile filiform tentacles. Gastrodermal diaphragm parenchymatic. Hydrocaulus stout, covered by thin perisarc, filled with parenchymatic gastrodermis, with long peripheral canals; aboral end of caulus with papillae turning more aborally into rooting filaments, rooting filaments composed of epidermis and solid gastrodermis, sometimes tips with non-ciliated statocysts. With or without asexual reproduction through constriction of tissue from aboral end of hydrocaulus.

Gonophores develop on blastostyles arranged in a whorl over aboral tentacles. Gonophores remain either fixed as sporosacs or are released as free medusae.

Medusa bell apex dome-shaped or pointed. Four marginal bulbs present, lacking long exumbrellar spurs. With a single tentacle or three short tentacles and one long tentacle that differs not merely in size, but also in structure. Manubrium thin-walled, sausage-shaped with flared mouth rim, reaching to umbrella margin. Cnidome comprises stenoteles, desmonemes, and haplonemes.

REMARKS: The above diagnosis corresponds largely to the scope of *Corymorpha* given in Petersen (1990), except that *Eugotoea* Margulis, 1998 is excluded. *Eugotoea* is here regarded as a synonym of *Rhabdoon*, a genus of uncertain affinity and discussed under "Capitata incerta sedis". The definition was therefore changed so that it now excludes medusae lacking marginal bulbs. Some modifications of Petersen's diagnosis were also necessary to exclude *Paragotoea* (see discussion at family level).

Ciliated statocysts in the anchoring filaments have only been observed for one *Corymorpha* species (Campbell, 1968, 1972; *C. palma*) and it is currently not known whether this is a feature of all *Corymorpha* species. Therefore, this feature should not be emphasized in the genus diagnosis.

Vervoort (2009) reviewed most species currently attributed to the genus *Corymorpha*. For special terms and an overview on their morphology see Allman

(1872), Campbell (1968, 1972), Petersen (1990), and Svoboda & Stepanjants (2001). The latter authors give also an overview of some *Corymorpha* species which they think should be separated into a distinct genus *Monocaulus*. Following Broch (1915; 1916), *Monocaulus* Allman, 1864a has usually been regarded as a synonym of *Corymorpha* M. Sars, 1935 (e. g. Bouillon *et al*., 2006). Allman (1864a) introduced the genus *Monocaulus* for *Corymopha glacialis* and *Corymorpha pendula* L. Agassiz, 1862. Apstein (1915) suggested that *Monocaulus imperator* Allman, 1885 should be the type species for the genus. However, this designation is invalid because *Monocaulus imperator* was not one of the species originally included in *Monocaulus* (see ICZN Article 69.1). Svoboda & Stepanjants (2001) then designated *Monocaulus groenlandica* Allman, 1876 as type species. Because also *M. groenlandica* was also not one of the original species for which *Monocaulus* was erected, Svoboda & Stepanjants made the assumption that Allman (1864a) had confounded *C. glacialis* and *C. groenlandica*. But the latter assumption is unfounded as Allman's (1864a) scope of *C. glacialis* is clearly based on Sars' (1860b) diagnosis. There are no indications that Allman had seen material of either *C. glacialis* or *C. groenlandica* before 1876. All these authors seem to have overlooked that Allman (1872: 396) himself made a type species designation by stating "The genus *Monocaulus* is constituted for the *Corymopha glacialis* of Sars, ..." Whatsoever, the principal differences of the two genera – branched versus unbranched blastostyles and medusae versus sporosacs – appear minimal and *Monocaulus* is here regarded as a synonym of *Corymorpha*, giving preference to a phylogeny-based system as presented in Petersen (1990) and following Bouillon *et al*. (2006).

Sassaman & Rees (1978) showed that the *Euphysora* must be referred to *Corymorpha*. Some names, like *Vannuccia* and *Lampra*, are invalid (see synonymy above).

The medusa *Corymorpha furcata* (Kramp, 1948) has not yet been observed in the ERMS zone, but it occurs only a few degrees south of it and may be discovered in the area sooner or later. For descriptions and diagnoses see Kramp (1959) or Schuchert (1996).

Key to species of *Corymorpha* of the ERMS zone:

1a only information on mature planktonic medusa available 6
1b polyp stage with gonophores present 2
2a gonophores released as medusae with functional tentacles 3
2b gonophores sporosacs or medusoids, usually retained on polyp 5
3a polyp large (5-15 cm), stem with about 20 longitudinal lines, long and branched blastostyles, medusae with pointed apical projection . . . . . . *C. nutans*
3b polyp small (< 5 cm), stem with < 20 lines, blastostyles short 4
4a oral tentacles moniliform and in one whorl, medusa with one club-shaped tentacle . . . . *C. forbesii*
4b oral tentacles filiform, medusa without apical projection, one moniliform tentacle . . . . *C. nana*
5a gonophores oblong medusoids, prominent bulbs but usually lacking tentacles . . . . *C. sarsii*
5b gonophores sporosacs with 4 radial canals, preserved polyps white *C. glacialis*

5c gonophores sporosacs without radial canals, preserved polyps reddish-brown . . . . *C. groenlandica*
6a mature medusa with one tentacle only 7
6b mature medusa with one large and three short tentacles 8
7a no apical process, terminal third of tentacles with club-like swelling . . . . *C. forbesii*
7b with pointed apical process and apical canal, tentacle moniliform . . . *C. nutans*
8a main tentacle with adaxial nematocyst buttons only . . . . *C. bigelowi*
8b main tentacle with ring-like nematocyst clusters . . . . *C. annulata*

Corymorpha nutans M. Sars, 1835 Figs 12-14

Corymorpha nutans M. Sars, 1835: 6, pl. 1 fig. 3. – Sars, 1877: 2, pl. 2 fig 25-28. – Hincks, 1868: 127, pl. 22 fig. 2. – Allman, 1871/1872: 208, 388, pl. 19. – Browne, 1896: 463, pl. 16 fig. 1. – Broch, 1916: 31, fig. G. – Rees, 1937: 743, figs 1-2. – Vervoort, 1946: 111, fig. 44. – Naumov, 1969: 226, figs 93-94. – Brinckmann-Voss, 1970: 12, figs 6-8, pl. 2 fig. 3. – Svoboda, 1973: 145, figs 1-2. – Petersen, 1990: 152, fig. 18. – Schuchert, 2001a: 40, fig. 27. – Bouillon *et al.*, 2004: 91, fig. 49A-C. – Vervoort, 2009: 768.
Steenstrupia rubra Forbes, 1848: 73, pl. 13 figs 1-2, medusa. – Browne, 1896: 464, synonym. – Neppi & Stiasny, 1913: 6.
Steenstrupia faveola Forbes, 1848: 74, pl. 13 fig. 2. – Browne, 1896: 464, synonym.
not *Corymorpha nutans*. – Sars, 1850: 135. [= *C. sarsii* Steenstrup, 1855]
Steenstrupia lineata Leuckart, 1856: 29, pl. 2 fig. 6. – Neppi & Stiasny, 1913: 6, synonym.
Steenstrupia cranoides Haeckel, 1864: 339. – Neppi & Stiasny, 1913: 6, synonym.
Steenstrupia galanthus Haeckel, 1879: 31. – Browne, 1896: 464, synonym.
Corymorpha appellöfi Bonnevie, 1901: 5, pl. fig 2. **new syn.**
Corymorpha nutnas. – Hartlaub, 1907: 76, figs 74-75. [misspelling]
Steenstrupia nutans – Kramp, 1926: 28, figs 23-28, chart V. – Russell, 1938b: 148, figs 1-7. – Russell, 1953: 84, figs 35A-D, 36, 37A-C, pl. 3 fig. 1, pl. 34 fig. 2, synonymy. – Kramp, 1959: 86, fig. fig. 32. – Kramp, 1961: 45.
Corymorpha appelloefi. – Vervoort, 2009: 63.

Type material examined: ZMUB number 10831; holotype of *Corymorpha apelloefi*; loc. Bergensskjorg., 40-50 m, not well preserved, stained red.

Other material examined: BELUM Md359; Scotland, Outer Hebrides, Scarba, SW Sgeir Nan Gabhar; 56.185° N05.74°W; 21 m; 14.07.1982; polyp with medusa buds. – BELUM Md503; Ireland, Donegal, Skuddagh Rock, St. John's Point; 54.566°33.97 N 08.463°W; 25 m; 06.06.1982; polyp with medusa buds. – ZMUC, without collection number; Denmark, Frederikshavn, 01.03.1931, coll. and id. P. Kramp, 12 fertile polyps. – MHNG INVE 48745; Norway, Raunefjord; 10-20 m; 14.06.2006; many hundreds of medusae; some used for DNA extraction; 16S **FN687546**. – England, Plymouth; 50.3339°N 04.1673°E; 0-5 m; 28.06.2007; 1 male medusa, used for DNA extraction; 16S **FN687547** – Atlantic, France, Roscoff; 48.730°N 04.000°W; 10-20 m; 05.06.2000; several fertile medusae, used for DNA extraction; 16S **AY512527**. – Mediterranean, France, Bay of Villefranche-sur-Mer; 43.686°N; 7.317°E; 0-70 m; 04.04.2005; 3 fertile medusae, used for DNA extraction; 16S **FN687548**.

Diagnosis: *Corymorpha* polyp 5-12 cm high, 30-60 long aboral tentacles and 50-100 short oral filiform tentacles in several closely-set whorls. Stem with 20 or more longitudinal lines. Gonophores on branched blastostyles, released as immature medusae with one tentacle and with pointed apical process. Mature medusa 4-5 mm high, with conical apical projection and long apical canal. Only one moniliform tentacle on large bulb, three marginal bulbs small, umbrella margin at right angles to vertical axis, exumbrella without nematocyst tracks.

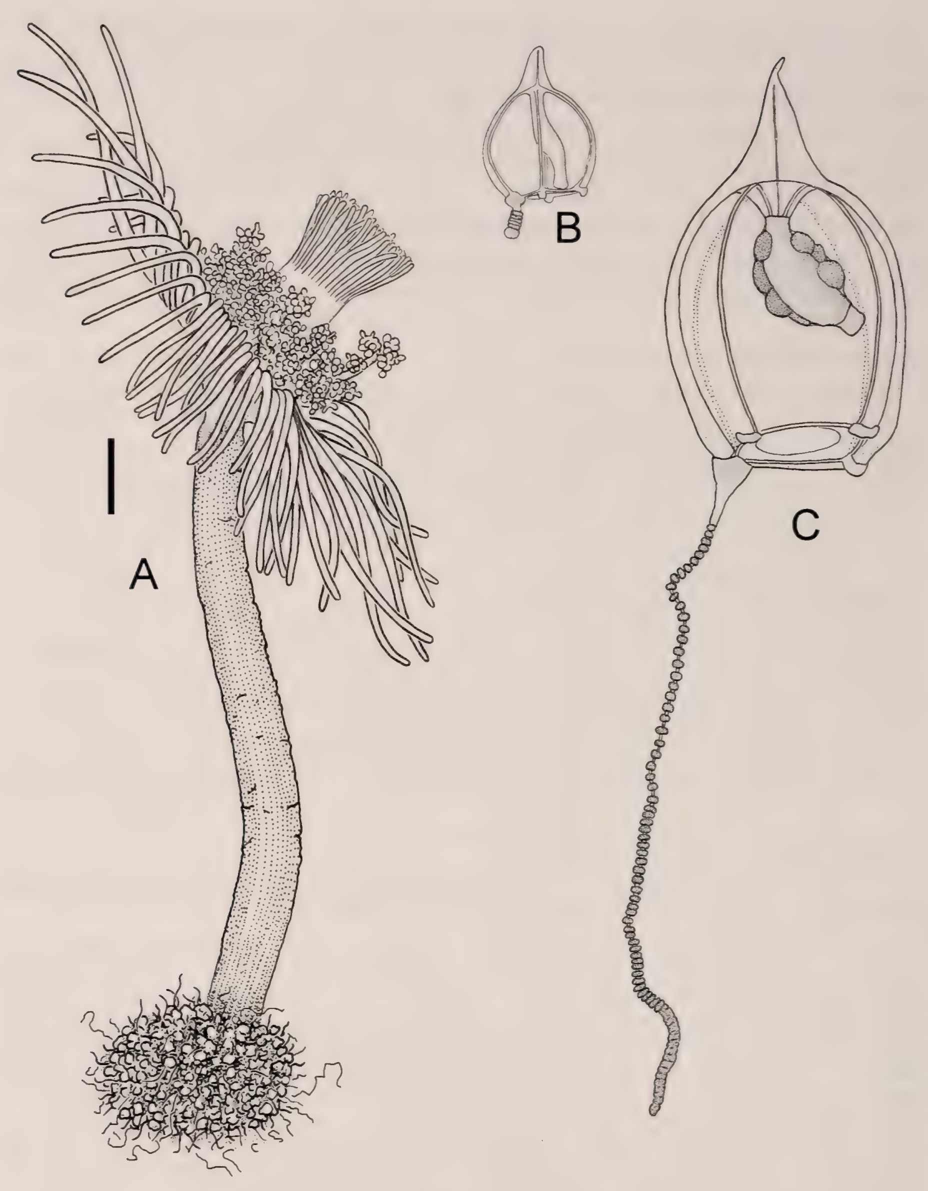


FIG. 12

Corymorpha nutans M. Sars, 1835. (A) Partially contracted polyp, with medusae buds, rooting filaments with entangled sand grains, combined after several preserved specimens from Denmark; scale bar 2 mm. (B) Newly liberated medusa, about 1.2 mm high, modified after Russell (1953). (B) Mature female medusa after life, bell height 4 mm.

DESCRIPTION: Hydroid solitary, not gregarious, base usually embedded in sediment. Hydranth body and stem distinctly separated, hydranth body relatively large, bends over towards one side, this feature being responsible for the hydroid's name (*nutans*, Latin for nodding).

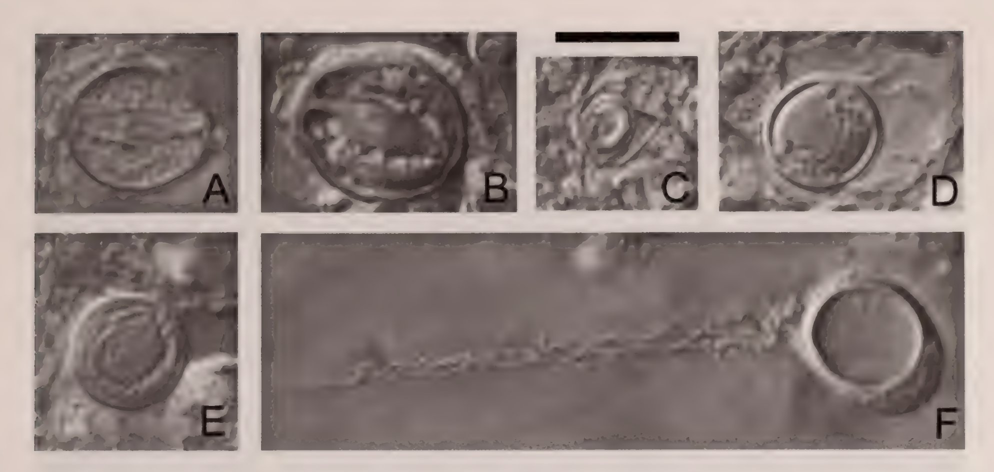


FIG. 13

Corymorpha nutans M. Sars, 1835; nematocysts of preserved polyp from Wales; scale bar 10 μm. (A) Smaller stenotele. (B) Larger stenotele. (C) Desmoneme. (D-F) Heterotrichous anisorhiza. (F) Discharged anisorhiza.

Stem stout, of variable length, contractile, proportion of hydranth size and stem length variable. Stem in living animals and when fully extended decreasing in diameter from level of basal filaments to hydranth for about a factor of two, basal end tapering. Perisarc very thin, membranous, only well visible in lowest part of stem. Stem interior filled by parenchymatic tissue and peripheral, longitudinal, ribbon-like gastrodermal canals. Canals number 20 or more when fully grown, clearly visible from outside as opaque, parallel lines along the surface of the more transparent rest of the stem. Canals occasionally branch to accommodate for the increasing stem-diameter and some transverse connection may also be present. Basal part of stem (buried in sediment) with outgrowths of tiny papillary projections along the longitudinal canals, gastrodermis of papillae connected to canals. Papillae more basally developing into long, fine filaments. Filaments adhesive, usually connected to sand grains, numerous and forming a tangled mass (rooting filaments).

Hydranth vasiform, quite translucent in life. Aboral tentacles long, 30 to 60 in one whorl, base laterally compressed. Around mouth of hydranth 50 to 100 (max. 200) oral tentacles in several closely set whorls. Gonophores develop on up to 12-30 (max. 50) long blastostyles that develop in one or two whorls just distal to the aboral tentacles. Blastostyles with short side-branches bearing clusters of 20 gonophores. Gonophores without envelope, developing into medusae, usually only a few per blastostyle ready to be released. Advanced medusa buds may have a bell margin which is either oblique or at a right angle to main axis, one long tentacle present before release of medusa.

Hydranth and stem usually translucent white or pale pink in colour.

Nematocysts stenoteles, anisorhizas, almond-shaped microbasic heteronemes of about the same size as stenoteles, desmonemes.

Newly liberated medusa similar to mature one but much smaller, gonads not visible yet, and only about five nematocyst clusters on tentacle. Pointed apical process and apical canal always present.



FIG. 14

Corymorpha nutans M. Sars, 1835: living polyps from the Island of Hitra, Norway, 12 m depth. Photo courtesy of Kåre Telnes (see /www.seawater.no).

Mature medusa with bell-shaped umbrella, distinctly higher than broad, with pointed conical apical process containing thin, long apical canal in its centre, apical process variable in form and size but always pointed; jelly moderately thick, with short gelatinous gastric peduncle. Umbrella margin at right-angles to vertical axis; no exumbrellar nematocyst tracks.

Manubrium spindle-shaped, somewhat shorter than height of bell cavity, in living animals always curved, direction of curve variable but often mouth bent away from tentacle, manubrium often with oil droplet near base. Mouth surrounded by a few nematocysts. Gonad surrounding entire length of manubrium, leaving only peduncle and mouth free. Females with a few large eggs only (approx. 10), amoeboid.

Four radial canals and ring canal present, fairly broad and well visible as relatively opaque and yellowish. Only one moniliform tentacle with 40-80 annular nematocyst clusters and one terminal cluster of same size, nematocyst clusters begin relatively close to bulb. Tentacular bulb is 2-3 times as large as other marginal bulbs, all bulbs with epidermal thickening containing nematocysts, in contracted or preserved medusae the epidermal part of the bulbs extend for a short distance up the exumbrellar surface like short exumbrella. No ocelli present. Rarely besides normal tentacle also other three bulbs with short, knobbed tentacle rudiments.

Colours of medusa (Russell, 1953): variable; marginal tentacle, marginal bulbs and stomach light pink, flecked with carmine, bright yellow, straw coloured or reddish brown; apical process often pinkish; radial canals and ring canal often with bright yellow pigment, sometimes brown granules at apex of stomach.

Nematocysts (Russell 1938b): stenoteles, spherical anisorhizas, oval microbasic euryteles, desmonemes.

Dimensions: Polyps releasing medusae may have heights from 2.5 to 20 cm (Svoboda, 1973), but usually the height is around 10-12 cm. Diameter of hydranth inclusive of the fully extended tentacles 2-6 cm. Preserved material shrinks considerably. Newly liberated medusa 1.1-1.4 mm high (Russell, 1953). Mature medusae 4-5 mm high and 3 mm wide, maximal height 6 mm. Egg size 0.23-0.25 mm (Brinckmann-Voss, 1970) or 0.28-0.30 mm (own observations on Norwegian medusae). For nematocyst measurements see Russell (1938b).

Additional data: The anchoring filaments of the polyps can occasionally turn into frustules and give rise to small, new polyps (Rees, 1957). Neppi & Stiasny (1913) and Petersen (1990: fig. 150B) observed that the atentaculate bulbs of the medusae may rarely bear short, rudimentary tentacles. The apical process of the medusae can have hair-like, unicellular processes (Hartlaub, 1907; Kramp, 1926), likely a culture artefact. Kramp (1926) describes the histology and microanatomy of the medusae. The differentiation of the egg is described by Müller, (1908). The early development was investigated by Rees (1937a), Werner (1959), and Brinckmann-Voss (1970). The embryo gets enclosed in a lenticular capsule. This resting stage can last up to 21 months. From this capsule a young polyp is hatched. The hatching depends on the water temperature, the development of polyp seems to be suppressed below 12°C and above 15°C (Brinckmann-Voss, 1970).

Biology: The hydroid lives rooted in the bottom sediment and may be found in silty sand, clean sand, or clean shell gravel (Russell, 1953; Teissier, 1965) in depths of 5 to 40 m, more rarely down to 100 m (Russell, 1957; Fey, 1970; Christiansen, 1972; Svoboda, 1973). It is rather sporadic in its occurrence and may be common in an area in one year and not another. It lives one season only (Svoboda, 1973).

The medusa is abundant in the northern as well as in the southern parts of its distribution within the European region. It keeps occurs within a short distance from the coasts. The seasonal occurrence is earlier in the southern than in the northern regions. At the southern British coasts, the medusa appears in March or April and has its main occurrence in May or June; at the coasts of Scotland it does not appear until May and is the most common in June; at the west coast of Norway it occurs in July, at the south-western coasts of Iceland in July and August (Kramp, 1926; Russell, 1953, 1957; Boyd *et al.*, 1973). The medusae disappear from the plankton starting from August to October, rarely November (Russell, 1953; Boyd *et al.*, 1973). In the Mediterranean (Naples), the medusa is much rarer and can be found in the plankton from January or February to May (Neppi & Stiasny, 1913; Brinckmann-Voss, 1970, 1987). The life duration of the medusa is less than 2 months (Russell, 1953). In the day-time, the medusae are usually caught below 20 m, at night they sometimes migrate upwards as far as 12 m and occasional species may even reach the surface (Russell,

1953). Lebour (1922, 1923) observed that they fed on copepods, crustacean larvae, *Sagitta*, fish eggs and young fish. The nudibranch *Cumanotus beaumonti* (Eliot) feeds on the polyps (Picton, 1991).

DISTRIBUTION: The polyp has been found along the coasts of north-western Europe from southern Brittany to Lofoten and the Norwegian coast (Kramp, 1926; Fey, 1970). Around Iceland the occurrence is restricted to the two great gulfs at the west coast (Broch, 1916). The polyp is present also in the Mediterranean (Brinckmann-Voss, 1970; Bouillon *et al.*, 2004).

In the north-western Atlantic, the medusa occurs from Morocco (Patriti, 1970) to Iceland and Norway, including the North Sea (Kramp, 1926, 1927, 1959; Russell, 1953). The medusa has also been caught in the western Mediterranean (Brinckmann-Voss, 1970; this study), the Adriatic Sea (Neppi & Stiasny, 1913), and the Black Sea (Thiel, 1935). Records from other oceans are doubtful. Type locality: near Glesvae, Sotra Island west of Bergen, Norway, 55-73 m depth.

REMARKS: This is a well known species presenting few problems, but also see under *C. sarsii*.

Corymorpha appelloefi Bonnevie, 1901 is very likely conspecific with *C. nutans*. Bonnevie separated it from the latter species on account of the reduced number of tentacles and the elongated upper part of the hydranth. A re-examination of the holotype made it evident that the tentacles are only broken off, likely during the collection procedure. The basal stumps remain, though. The elongated hydranth is evidently also a collection artefact. There is otherwise nothing that would distinguish this material from *C. nutans*.

Corymorpha forbesii (Mayer, 1894) Fig. 15

Hybocodon forbesii Mayer, 1894: 236, pl. 1 fig. 1. – Mayer, 1910: 42, pl. 1 fig. 8, pl. 2 fig. 3. – Vanhöffen, 1913: 414. – Uchida, 1927: 193: fig. 30.
Hybocodon sp. Menon, 1932: 5, pl. 1 fig. 1.
Hybocodon forbesi. – Kramp, 1959: 87, fig. 36. – Kramp, 1961: 42. – Kramp, 1968: 13, fig. 22. [incorrect spelling]
Hybocodon forbessi. – Nair, 1951: 50, pl. 1 fig. 1. [incorrect spelling]
? *Hybocodon forbesi*. – Allwein, 1967: 122.
Vannuccia forbesii. – Brinckmann-Voss, 1967: 1, figs 1-6. – Brinckmann-Voss, 1970: 14, figs 9-11, pl. 1 figs 1-2. – Schmidt, 1973a: 17. – Bouillon, 1978b: 268, fig. 8.3-4. – Bouillon *et al*,. 2004: 93, fig. 49K-L.
Vannuccia forbesii f. *kanti* Bouillon, 1978a: 136.
Corymorpha forbesii. – Schuchert, 1996: 103, fig. 60a-c. – Vervoort, 2009: 765.

MATERIAL EXAMINED: MHNG INVE 29471; New Zealand, between Auckland and Leigh; collected February 1997 by A. Freudenthal; 3 medusae. – BMNH 1974.11.21.4; Italy, Naples; November 1962; material of Brinckmann-Voss (1967); 3 medusae liberated from hydroid; hydroid accompanying this sample is lost. – ZMUC, without registration number; USA, North Carolina; 06.11.1964; 1 immature medusa; leg. J. Allwein (material Allwein, 1967); has pointed apical process and apical canal, may be other species.

DIAGNOSIS: *Corymorpha* polyp with moniliform oral tentacles. Medusa bilaterally symmetric, bell margin may be slightly oblique, no apical process, with one large, single, rather stiff tentacle, terminal third with club-like swelling, bulb opposite tentacle larger than the two other atentacular bulbs.

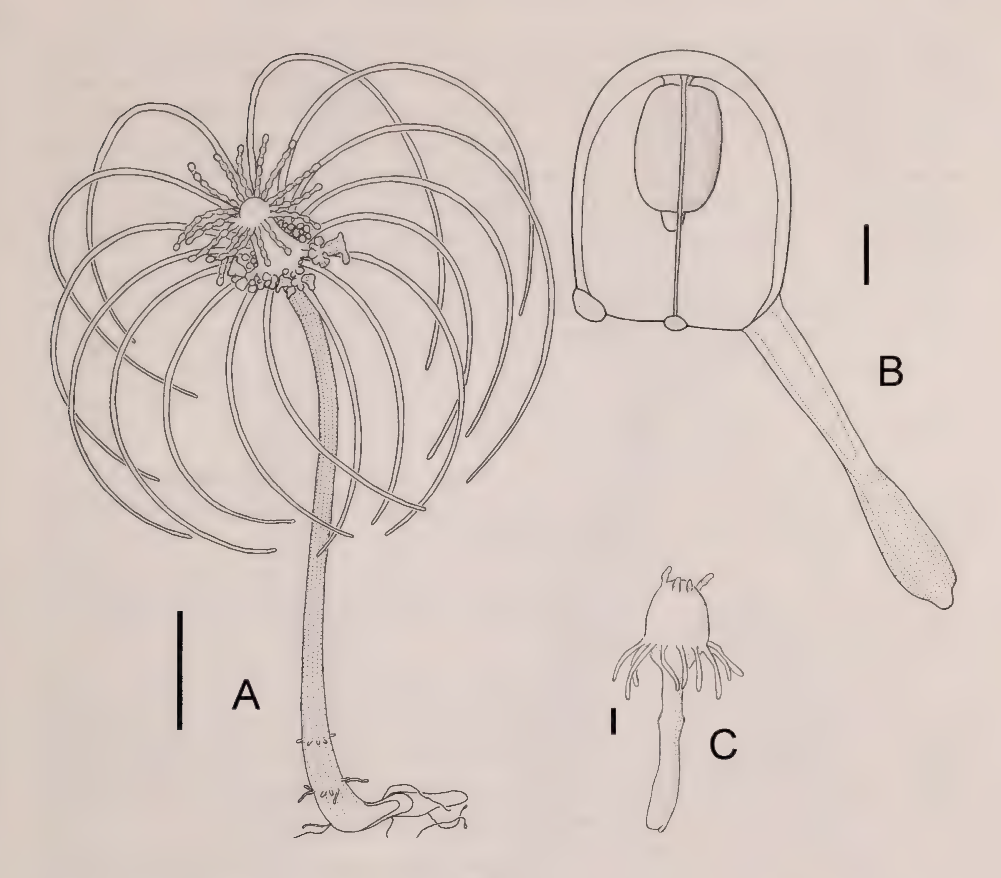


FIG. 15

Corymorpha forbesii (Mayer, 1894) (A) Polyp with medusa buds, scale bar 2 mm, drawn after colour plate in Brinckmann-Voss (1970). (B) Lateral view of medusa, after preserved medusa from New Zealand, scale bar 0.2 mm, from Schuchert (1996). (C) Young polyp derived from asexual budding, scale bar 0.2 mm, modified after Brinckmann-Voss (1970).

DESCRIPTION (Mayer, 1910; Brinckmann-Voss 1967, 1970; own data): Solitary hydroids, height variable, caulus and hydranth well separated. Caulus covered by filmy perisarc that extends slightly onto the hydranth body, with 3-4 gastrodermal longitudinal canals, at basal end rows of papillae budding along gastrodermal canals, growing into numerous, long rooting filaments. Hydranth vasiform, with one oral and one aboral whorl of tentacles. Oral tentacles numbering 12-14, moniliform with 4-6 nematocyst clusters. Aboral whorl with 16-20 filiform tentacles. Medusae buds develop in clusters on short blastostyles originating above the aboral tentacles. Medusae buds naked. Aboral end of polyp within perisarc tube may constrict off parts that grow into new polyps (asexual multiplication).

Young medusae resemble adult ones, only gonads are not developed yet. Gonads start to develop soon after liberation.

Adult medusa with bell-shaped umbrella, higher than wide, jelly evenly thin, without apical process, no exumbrellar nematocyst tracks. Bell margin sometimes

slightly oblique. Manubrium cylindrical, length 1/2 to 2/3 of bell height, mouth simple, round. Gonads usually encircle manubrium for almost all its length, in some animals a free upper part (forma *kanti*). Usually with a single tentacle only, about as long as the bell-height. Tentacle relatively stiff, voluminous, hollow in proximal half, terminal region except very distal end with a swollen epidermis containing many nematocysts, giving it a club-like appearance. In some animals there may also be an additional, thin, short tentacle on the bulb opposite the large tentacle. Four narrow radial canals and circular canal present. Marginal bulbs present on perradial sites other than occupied by tentacle. Marginal bulb opposite large tentacle slightly larger than the two other atentaculate ones, no distinct bulb where large tentacle is attached.

Colours: The gastrodermis of the large tentacle is yellow streaked with red.

Nematocysts: two types of stenoteles, desmonemes, spherical anisorhizas (or perhaps isorhizas), almond-shaped microbasic euryteles.

Dimensions: Hydroids up to 2-3 cm high. Newly liberated medusa 1.8-2 mm high. Adult medusa 2.5- 3 mm high. For illustrations and dimensions of the nematocysts see Bouillon (1978b) or Schuchert (1996).

Biology: The hydroid was found once in mud at 30 m depth (Brinckmann-Voss, 1970). The medusa can be caught close to the water surface, but it is usually rare, except perhaps in the Caribbean.

Distribution of Medusa: Tortugas and Bahamas (Mayer, 1894), Brazil (Navas-Pereira, 1980), Mediterranean (Brinckmann-Voss, 1970), Red Sea (Schmidt, 1973a), Seychelles (Bouillon, 1978a), India (Nair, 1951), Vietnam (Kramp, 1962), Papua New Guinea (Bouillon, 1978b), southern Japan (Uchida, 1927), and New Zealand (Schuchert, 1996). Type locality: Nassau Harbour, Bahamas.

Remarks: Following Petersen (1990), this species is here included in the genus *Corymorpha*. Other authors used the genus name *Vannuccia* Brinckmann-Voss, 1967, but it is preoccupied by *Vannuccia* Marcus, 1948 [Platyhelminthes]. If it should be necessary to remove the species from the genus *Corymopha*, then the genus *Altairina* Vargas Hernandez & Ochoa-Figuera, 1991 is available.

Bouillon (1978a, c) observed that some of his medusae had only part of the manubrium covered by the gonad. He named this form "f. *kanti*". The name has no official value as form names proposed after 1961 are not recognized as species level names by the ICZN [article 15.2].

The specimen from North Carolina (material Allwein, 1967) had a pointed apical process and an apical canal, it may thus may belong to another species.

Corymorpha nana Alder, 1857 Fig. 16

? *Hydractinia*. – Johnston, 1847: 461, fig. 79a.
Corymorpha. – Johnston, 1847: 461, fig. 79b.
Corymorpha nana Alder, 1857a: 108, p 9 figs 7-8. – Alder, 1862: 233, pl. 11. – Hincks, 1868: 130, pl. 22 fig. 3. – Bonnevie, 1899: 22, pl. 1 fig. 7. – Hartlaub, 1907: 81. – Rees, 1938: 25. – Cornelius & Garfath, 1980: 275. – Russell, 1953: 84. – Svoboda & Stepanjants, 2001: 58. – Vervoort, 2009: 768.
Halatractus nanus. – Allman, 1872: 391.
Halatractus (*Corymorpha*) *nanus*. – Stechow, 1912a: 404, fig 1, pl 7.

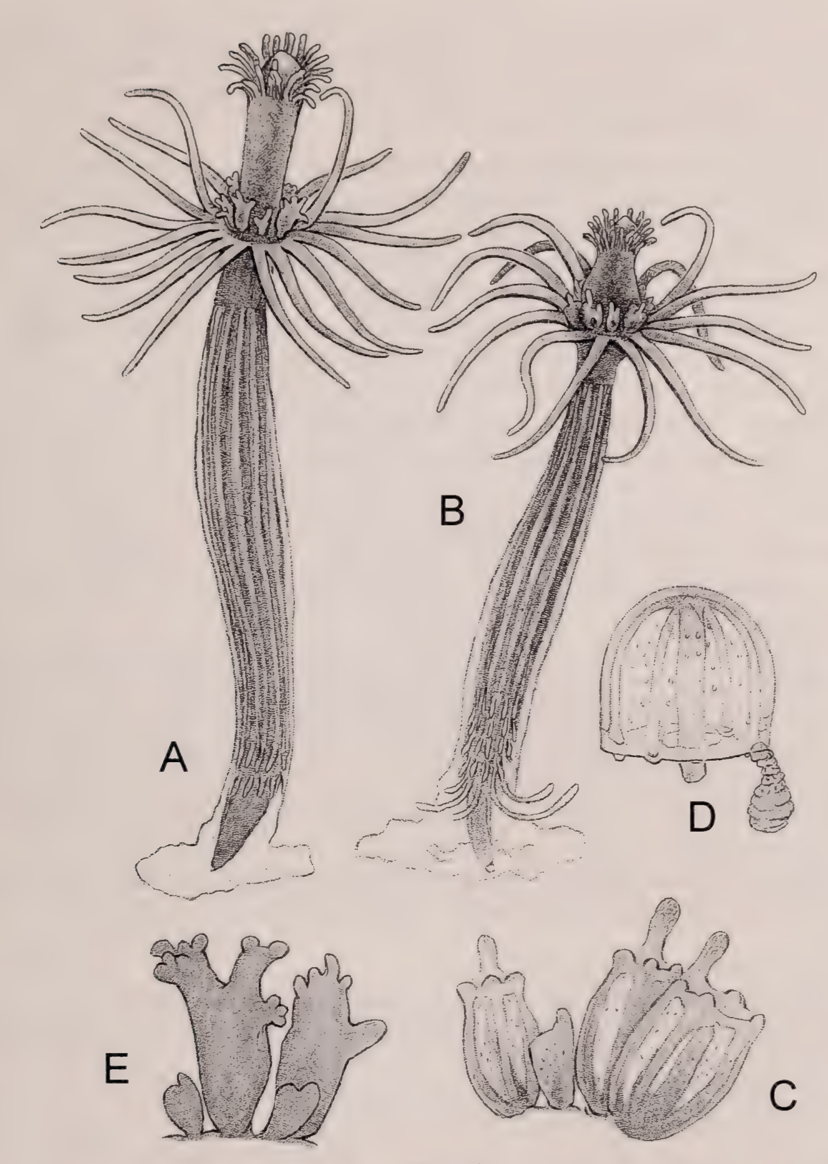


FIG. 16

Corymorpha nana Alder, 1857; from Alder (1862), based on non-type material. (A) Polyp with blastostyles. (B) Polyp with medusa buds. (C) Medusa buds, enlarged. (D) Newly liberated medusa. (E) Blastostyles of animal shown in A (note that the identification as blastostyles is an interpretation of later authors).

DIAGNOSIS: Like *C. nutans*, but much smaller (10-18 mm high), 16-18 short oral tentacles in two indistinct whorls, less than 20 stem canals, gonophores arise on 10-15 short, stubby, mostly unbranched blastostyles. Newly liberated medusa with one tentacle, rounded umbrella without apical process or apical canal, yellowish radial canals and bulbs.

Distribution: Northumberland (England; Alder, 1857a, 1862), Norwegian coast of the Barents Sea (271 m; Bonnevie, 1899), ?Plymouth (English Channel; Stechow, 1912b). Type locality: Newbiggin, Northumberland "among sea-refuse brought in by the fishing boats" (Alder, 1857a).

Remarks: *Corymorpha nana* is insufficiently known and some authors doubted its validity (e. g. Hartlaub, 1907) and considered it as conspecific with *Euphysa aurata*. Cornelius & Garfath (1980) re-examined the type specimen and found that it had dried out. They cite a personal communication of C. Edwards claiming that the *C. nana* likely belongs to *E. aurata*. Other authors rejected the idea (e. g. Rees, 1938; Russell, 1953). The longitudinal striation of the caulus – also mentioned in the first description – makes it unlikely that this species belongs to *Euphysa*. The more detailed description and illustration in Alder (1862, see also Fig. 16) leave no doubt that this is a *Corymorpha* species: the longitudinal stem-channels and the basal papillae are obviously not compatible with a *Euphysa* polyp. Alder (1862) thought that the two polyps he had at hand differed in their mode of reproduction, as one released medusae which were formed directly on the hydranth body, while the other had "tuberculated lobes" which did not develop medusae in the 10 days he kept the polyps alive. Bonnevie (1899) correctly recognized that these lobes are likely short blastostyles, an interpretation I share with her.

Corymorpha nana thus closely resembles *C. nutans* – a fact also emphasized by Alder (1862) – except for its size and the medusae which are liberated without an apical process (comp. Figs 12B and 16DC). Nothing is known about the mature medusa. The only corymorphid medusa known from the region for which the polyp is not known is *Euphysa tentaculata*, which can also have a single tentacle (see below). This medusa is thus a good candidate, but more research is clearly needed to establish *C. nana* firmly as a distinct species.

Stechow (1912a) observed only a very small animal of 3.5 mm that had no medusa buds yet. This identification must be considered as tentative only.

Corymorpha sarsii Steenstrup, 1855 Figs 17-18

Corymorpha nutans. – Sars, 1850: 135. [not *Corymorpha nutans* M. Sars, 1835]
? *Amalthaea uvifera* O. Schmidt, 1852: 13, pl 9 figs 2 & 2a. – Allman, 1872: 393. – Broch, 1916: 30, synonym.
Corymorpha Sarsii Steenstrup, 1855: 48.
Corymorpha uvifera. – Sars, 1860b: 344. – Vervoort, 2009: 772.
Amalthaea Sarsii. – Allman, 1872: 393. – Stechow, 1912b: 338, pl 12 fig 2.
Corymorpha sarsii. – Sars, 1877: 4, pl. 2 figs 18-24, pl. 6 figs 9-23. – Bonnevie, 1898: 476. – Jäderholm, 1909: 42. – Vervoort, 2009: 771.
Amalthaea vardöensis Loman, 1889: 271, fig. 5, pl. 13. – Stechow, 1912b: 339, pl. 12 figs 3-5.
Corymorpha vardöensis. – Broch, 1916: 29, synonym. – Stechow, 1934: 197, synonym.
not *Amalthaea amoebigera* Hackel, 1879: 38, pl. 1 figs 10, 11. [? *Pennaria disticha*]

Type material examined: ZSM 20040172, slides ZSM 20060700 through 20060711; syntypes of *Amalthaea vardoensis* Loman, 1889; Norway, Busse Sund, Vardø, depth 2-4 m; 4 fertile polyps in alcohol and slides.

Other material: ZMO B1109; Norway, Lofoten, Skraaven; material described by Sars (1877), collected in summer 1866 in a depth of 22-37 m; preserved in alcohol; about 8 fragmented but otherwise relatively well preserved polyps with advanced medusoids. – ZMO B1106; as *Corymorpha sarsii*; Norway, Hasvik; det. K. Bonnevie; about 5 fertile polyps in alcohol. –

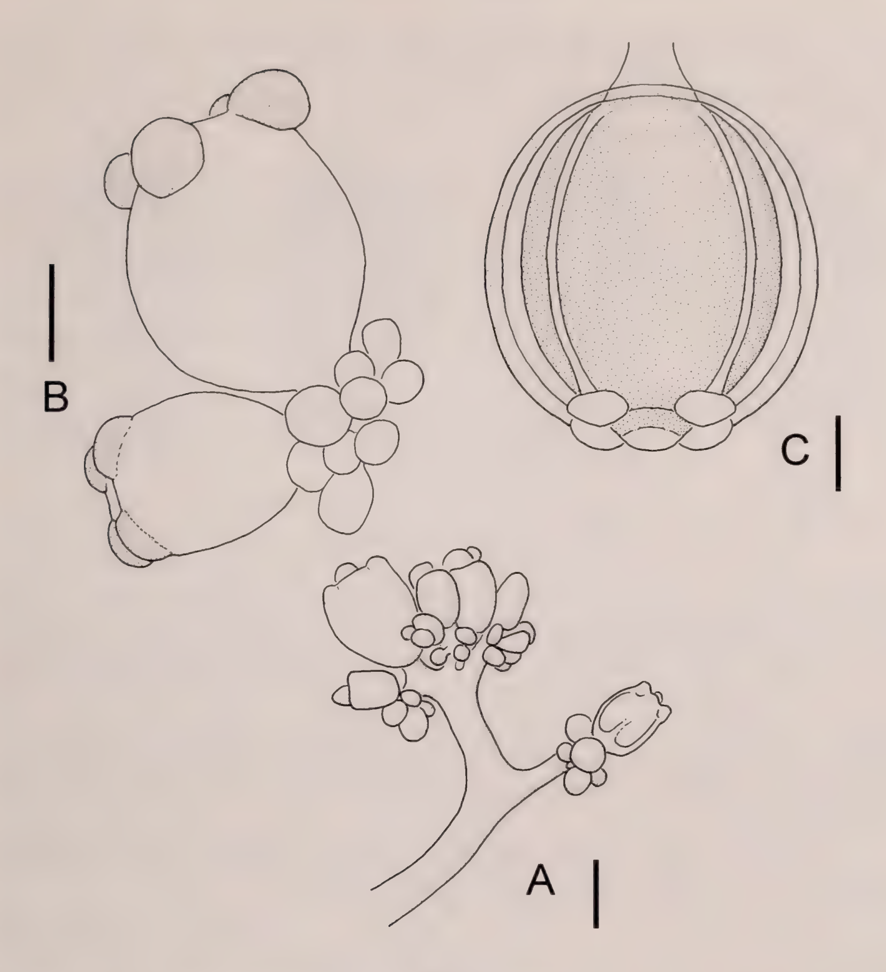


FIG. 17

Corymorpha sarsii Steenstrup, 1855. (A) Blastostyle, after preserved material from Hammerfest, Norway; scale bar 0.5 mm. (B) Cluster of juvenile gonophores, the two most advanced show the characteristic, prominent marginal bulbs of the future medusoid, scale bar 0.2 mm, after preserved material from Hasvik, Norway. (C) Schematized, immature medusoid gonophore, scale bar 0.2 mm, after preserved material from Hammerfest. Note that fully mature medusoids are more elongated (Fig. 18).

ZSM 20041436, slides ZSM20060214 through 20060216; as *Corymorpha sarsii*; Norway; Hammerfest; 3 fertile polyps in alcohol and slide preparations, collected 1890; leg. Jägerskiöld; likely material described in Stechow (1912b) and Jäderholm (1909). – ZSM 20041437, slides ZSM 20061436, ZSM 20060199-2006208, ZSM 2006010-2006213; as *Corymorpha sarsii*; Black Sea, Bulgaria, Marine Biological Station of Varna, depth 40 m; collected 1934 by Paspaleff; 4 polyps in alcohol and serial sections on slides; all with immature gonophores; material of Stechow (1934). – MHNG INVE 68950; Black Sea, Turkey, Bay of Sinop; depth 3 m; fertile male collected 26.03.2010 by Murat Sezgin.

DIAGNOSIS: *Corymorpha* species resembling *C. nutans*, but gonophores are medusoids which remain attached to the polyp, blastostyles branched. Medusoids

2-4 mm in height, oblong when mature, lacking usually tentacles, with four conspicuous, identical bulbs, with velum, wide umbrella with mesogloea, functional subumbrellar musculature, manubrium may be protruding through velar opening, bell margin at right angle to longitudinal axis.

DESCRIPTION (own data; Stechow, 1912b): Trophosome indistinguishable from *C. nutans* (see above) as falling within its range of variability, likely not attaining the same maximal heights; about 20 stem canals, 30-60 aboral tentacles, up to 100 oral tentacles in several whorls, 8-20 blastostyles. Blastostyles often relatively short, usually branched dichotomously, gonophores grouped in terminal regions of branches. Developing gonophores round to oval, with clearly visible radial canals and four bulbs, all four bulbs at distal end, proximal side of bud without pointed projection. The marginal bulbs are formed at an early stage and are rather prominent (Fig. 17A-B). Most examined specimens had young gonophores only. Polyp likely without distinct colour, translucent.

Mature gonophores large medusoids, usually remaining attached to blastostyles, umbrella elongated bullet-shaped, ratio of height to width reaching 2, umbrella formed as in free medusae, composed of mesogloea and functional subumbrellar musculature, mesogloea at apex somewhat thickened but without distinct apical process, with umbilical canal, with relatively small velum. Manubrium large, filling nearly the subumbrellar cavity, in males often protruding through velar opening, spindle-shaped, in males almost entirely surrounded by an uninterrupted gonad, in females with few (~10) amoeboid eggs resulting in an uneven contour of the gonad. Four radial canals present, opaque white, ending in four conspicuous marginal bulbs, sometimes all four bulbs quite projecting, suggestive of tentacle stumps, very rarely one bulb with a short, thin tentacle (Fig. 18C).

Colours: bulbs pale reddish, manubrium of males reddish-brown to light yellow, manubrium of females rose coloured and more transparent.

DIMENSIONS (Sars, 1877; living material): Polyp up to 9 cm, sexual reproduction commences at a size of 1 cm (Sars, 1877). Blastostyle length 1/5 to 1/6 of aboral tentacle length. Immature gonophores recognizable as medusoids when reaching 1 mm, fully developed medusoids up to 4 mm in length.

OTHER DATA: Sars (1877) artificially detached a mature medusoid and observed that is was able to swim like a normal medusa for quite some time. He claims that the medusoids are likely not released, except under abnormal conditions (e.g. strong water movement).

BIOLOGY: Recorded from depths of 2 to 91 m, more likely usually occurring below 20 m. The bottom types are sand, coarse sand, clay mixed with sand, shell gravel and fragments of coralline algae, likely preferring places with a constant current (Sars, 1877; Loman, 1889; Stechow, 1912b).

DISTRIBUTION: Northern Norway, from Lofoten Islands to the Varangerfjord in the Barents Sea (Schmidt, 1852; Sars, 1877; Loman, 1889; Jäderholm, 1909). Also recorded from the Black Sea (Stechow, 1934; this study). Type locality: 0.5 miles east of Reine, Vestfjorden, Lofoten Islands, Norway; 73-91 m depth.

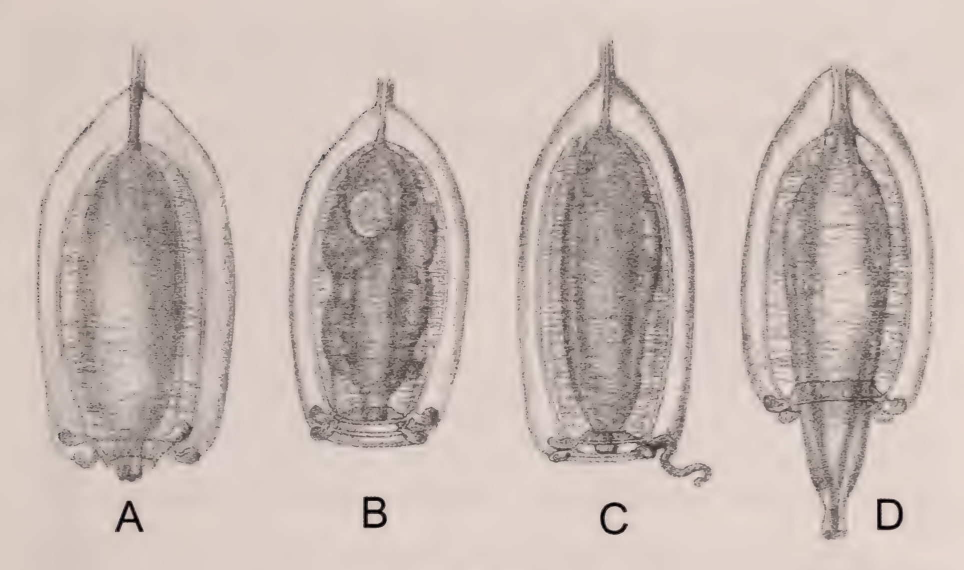


FIG. 18

Corymorpha sarsii Steenstrup, 1855; after Sars (1877), medusoids likely drawn after living specimens. (A) Male medusoid. (B) Female medusoid. (C) Medusoid with tentacle rudiment. (D) Medusoid with protruding manubrium.

REMARKS: Following Broch (1916) and Stechow (1934), I regard *C. vardoeensis* as conspecific with *C. sarsii*; they are in fact indistinguishable. *Amalthaea uvifera* O. Schmidt, 1852 is insufficiently described but very likely also identical with *C. sarsii* (Broch, 1916). The name *Amalthaea uvifera* is actually older than *C. sarsii*, but has not been used after its original publication to name other material besides the type material. In the interest of nomenclatural stability it should thus not replace the better known *C. sarsii*.

Hartlaub (1907) noted that *Amalthaea amoebigera* Haeckel, 1879 bears some resemblance to the medusoids of *C. sarsii*. Haeckel's medusoid from the Canary Islands offers too few diagnostic traits to be identifiable and must be considered an indeterminate species. Most probably it was only a detached medusoid of *Pennaria disticha* (cf. Schuchert, 2006).

Corymorpha sarsii has been regularly found only in northern Norway, qualifying it thus as an Arctic species. The purported occurrence in the Black Sea (Stechow, 1934) is thus rather surprising. I had the opportunity to examine Stechow's material and it indeed looks like *C. sarsii*. The gonophores are clearly medusoids resembling Fig. 17B. However, none of them is fully developed and in the histological sections I could not find any one with developed gonads. A recetly collected specimen from the Turkish coast of the Black Sea (MHNG INVE 68950), however, was fully fertile and confirmed the presence of a *C. sarsii*-like hydroid in the Black Sea. Despite the morphological similarity, I suspect that we are dealing with two different biological species. The status of the *C. pendula* from the east coast of the USA, a species resembling closely *C. sarsii*, remains also to be resolved.

Corymorpha sarsii has not often been found and remains somewhat incompletely described, e. g. no information on the cnidome is available or if the medusoids are able to feed.

Specimens having only young gonophores might be difficult to distinguish from *C. nutans* and *C. glacialis*. It appears that the four bulbs are larger and more prominent.

Of all described specimens, only the material of Sars (1877) had fully developed medusoids. The rarity of fully mature medusoids could indicate that the development takes a relatively long time.

Corymorpha glacialis M. Sars, 1860 Figs 19-23

Corymorpha glacialis M. Sars, 1860a: 96. – M. Sars, 1860b: 345. – Sars, 1877: 11, pl. 1 figs 14-22, pl. 2 figs 1-17. – Bonnevie, 1898: 476. – Bonnevie, 1899: 23. – Broch, 1916: 32. – Naumov, 1969: 231, figs 99-100. – Schuchert, 2001a: 38, fig. 25. – Vervoort, 2009: 765.
Monocaulus glacialis. – Allman, 1872: 396. – Svoboda & Stepanjants, 2001: 66, fig. 1c1-3.
Amalthaea islandica Allman, 1874: 179. – Allman, 1876: 256, pl. 9 figs 5-6. – Broch, 1916: 32.

Type material examined: Syntypes, ZMO B1103 (seen material loaned to ZMUC in 1999).

Other material examined: MHNG INVE 67049; Faroe-Shetland Channel, 61.2669°N 02.9968°W, 1050 m, collected 19.10.2009 by Daniel Jones with ROV; large fertile female. – MHNG INVE 67050; Faroe-Shetland Channel, 61.2669°N 02.9968°W, 1050 m, collected 19.10.2009 by Daniel Jones with ROV; large fertile male; 16S sequence **FN687549**. – Other material listed in Schuchert (2001a).

Diagnosis: *Corymorpha* polyps 4-14 cm in height, 80-100 oral tentacles, 40-75 long aboral tentacles, blastostyle unbranched, gonophores sporosacs with four shallow distal bulbs, sometimes with visible radial canals, no velum, no mesogloea, manubrium and gametes fill sporosac completely. Preserved material beige.

Description of animals from less than 200 m depth (own data and Sars, 1877): Hydroid solitary, not gregarious, base usually embedded in sediment. Hydranth body and stem distinctly separated, hydranth body relatively large, tentacles relatively long (up to ½ of stem height).

Stem stout, of variable length, contractile. Stem decreasing in diameter from level of basal filaments to hydranth for about a factor of two, basal end tapering. Perisarc very thin, membranous, only clearly visible in lowest part of stem. Stem interior filled with parenchymatic tissue and peripheral, longitudinal, ribbon-like gastrodermal canals. Canals number 20-24, clearly visible from outside as semi-opaque parallel lines along the surface of the more transparent rest of the stem. Canals occasionally branch to accommodate for the increasing diameter and some transverse connection may also be present. Basal part of stem (buried in sediment) with outgrowths of tiny papillary projections in a double row along the longitudinal canals. Papillae more basally developing into long, fine filaments. Filaments adhesive, usually connected to sand grains, numerous and forming a tangled mass (rooting filaments).

Hydranth vasiform, quite translucent in life. Aboral tentacles long, 40-50 in one whorl, laterally compressed. Around mouth of hydranth 50 to 100 short oral tentacles in three or more closely set whorls. Gonophores develop on 20-35 long blastostyles that develop just distal to the aboral tentacles. Blastostyles usually unbranched and rod-like, rarely with a short side branch (1 per hydranth), conspicuous rosy colour, gono-

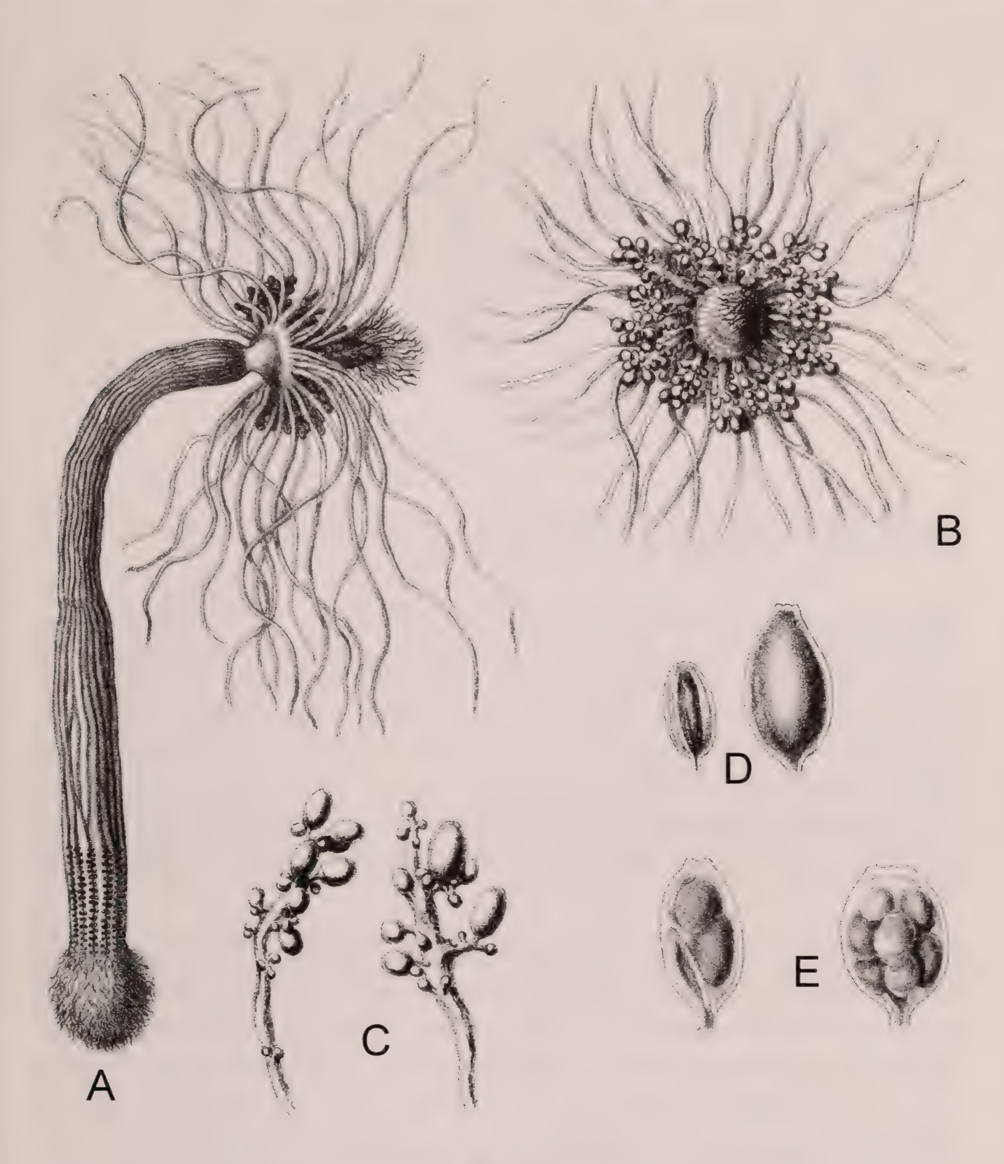


FIG. 19

Corymorpha glacialis M. Sars, 1860; from Sars (1877). (A) Entire polyp in lateral view. (B) Polyp seen from oral side. (C) Blastostyles, right a rare branched one. (D) Male sporosacs of different developmental stages (E) Female sporosacs with developing embryos.

phore number per blastostyle relatively small (up to 10), gonophores on distinct stalk, distributed either solitary or in small clusters on blastostyle, with a developmental gradient from proximal to distal, the most advanced at the end.

Gonophores are sporosacs, gonads and spadix (manubrium) fill sporosac entirely and thus no vestigial subumbrella present, without subumbrellar musculature or velum, radial canals (or strands, or parts of) can be visible or not, usually lumen of

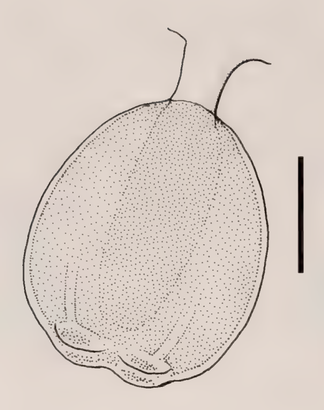


FIG. 20
Corymorpha glacialis M. Sars, 1860; after preserved material from Iceland, male sporosac with visible vestiges of radial canals or strands, scale bar 0.5 mm.

radial canals so small that canals are indiscernible, distal end of radial canals with four shallow distal bumps containing nematocysts, between the bumps a simple opening for the release of the gametes, female with 1-10 eggs that develop within sporosacs.

Preserved polyps white to beige. Living polyps nearly colourless and transparent, stem with white opaque longitudinal lines, blastostyles rose coloured, male sporosacs opaque rose-yellowish.

DIMENSIONS: Reproductive polyps 2.5 to 6 cm, reportedly up to 12.5 cm high (Sars, 1877); length oral tentacles 1-2 mm, aboral tentacles up to 3 cm; sporosacs 1 to 1.5 mm.

DEEP WATER FORM: Like above, but height larger (up to 14 cm), stem much thicker (9 mm at about 1 cm below hydranth), with up to 45 longitudinal canals in stem; hydranth in aboral view kidney-shaped (Fig. 21A), aboral tentacles up to 75, up to 60 blastostyles, blastostyles unbranched (exceptionally branched once), blastostyles bandlike flattened, gonophores in clusters; female sporosacs up to 1.9 mm long and 1.5 mm wide, few lobed eggs, male sporosacs up to 1.8 mm long and 1.2 mm wide. Alcohol preserved nematocysts: large stenoteles (20)x(17-18)μm; small stenoteles (13-15)x(10.5-11)μm; desmonemes (7.5-8.5)x(4.5-5.5)μm; round heterotrichous anisorhizas (18-21)x(16.5-18)μm; oval ? heteronemes (not see discharged) (12-12.5)x(3.5-4.5)μm.

OTHER DATA: The animals are gonochoristic (Sars, 1877). The development of embryos takes place in the sporosac, resulting in 2-mm-sized polyps, the animals are thus viviparous (Naumov, 1969).

BIOLOGY: Occurs in depths of 5-1050 m (Sars, 1877; Naumov, 1969; Schuchert, 2001a; Svoboda & Stepanjants, 2001; new data).

DISTRIBUTION: Arctic species of the North Atlantic penetrating into northern boreal regions, the southern limit being the Faroe Islands. Recorded from western Greenland, Iceland (north and east coast), Faroe Islands, Spitsbergen, northern

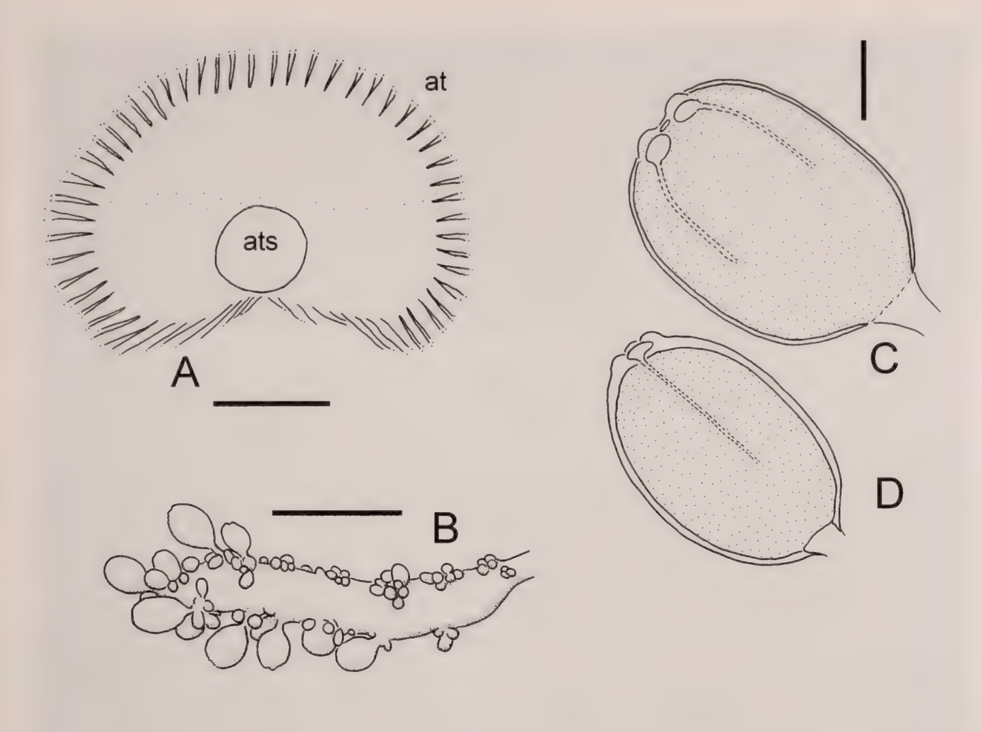


FIG. 21

Corymorpha glacialis M. Sars, 1860; deep water form from the Faroe-Shetland Channel. (A) Schematic view of the underside of the hydranth, tentacles cut, note kidney-shaped contour; *at* aboral tentacles, *ats* attachment site of caulus; scale bar 1 cm. (B) Typical blastostyle of female animal; scale bar 1 cm. (C) Female sporosac, scale bar 0.5 mm. (D) Male sporosac, same scale as C.

Norway, White Sea, Barents Sea, Kara Sea, and Laptev Sea (Sars, 1877; Broch, 1916; Naumov, 1969; Schuchert, 2001a; Svoboda & Stepanjants, 2001). Type locality: near Vadsø, Varangerfjord, Barents Sea.

REMARKS: The publication year of Sars' first description is 1860 and not 1859 (Bedot, 1910).

Sars (1877) states that the sporosacs lack radial canals, but have four distal bumps resembling rudimentary bulbs. The gonophores are never released. Bonnevie (1898: 476) examined the type specimens of *C. glacialis* and made thin sections of the sporosacs. She observed that radial canals are present, but their lumen is so small that they are difficult or impossible to see macroscopically. In some specimens examined for this study, the distal parts of the radial canals were rather well visible (Fig. 20). They were more radial strands than radial canals and likely reduced in the more proximal part of the sporosac (Fig 21C-D). A circular canal or strand is always absent.

Corymorpha glacialis resembles *C. groenlandica* and *C. sarsii*. If no radial canals are visible, preserved *C. glacialis* can nevertheless be distinguished from *C. groenlandica* due to the brown-red colour of the latter and the white colour of the former. Additionally, the nematocysts are different (comp. Figs 22 and 26),

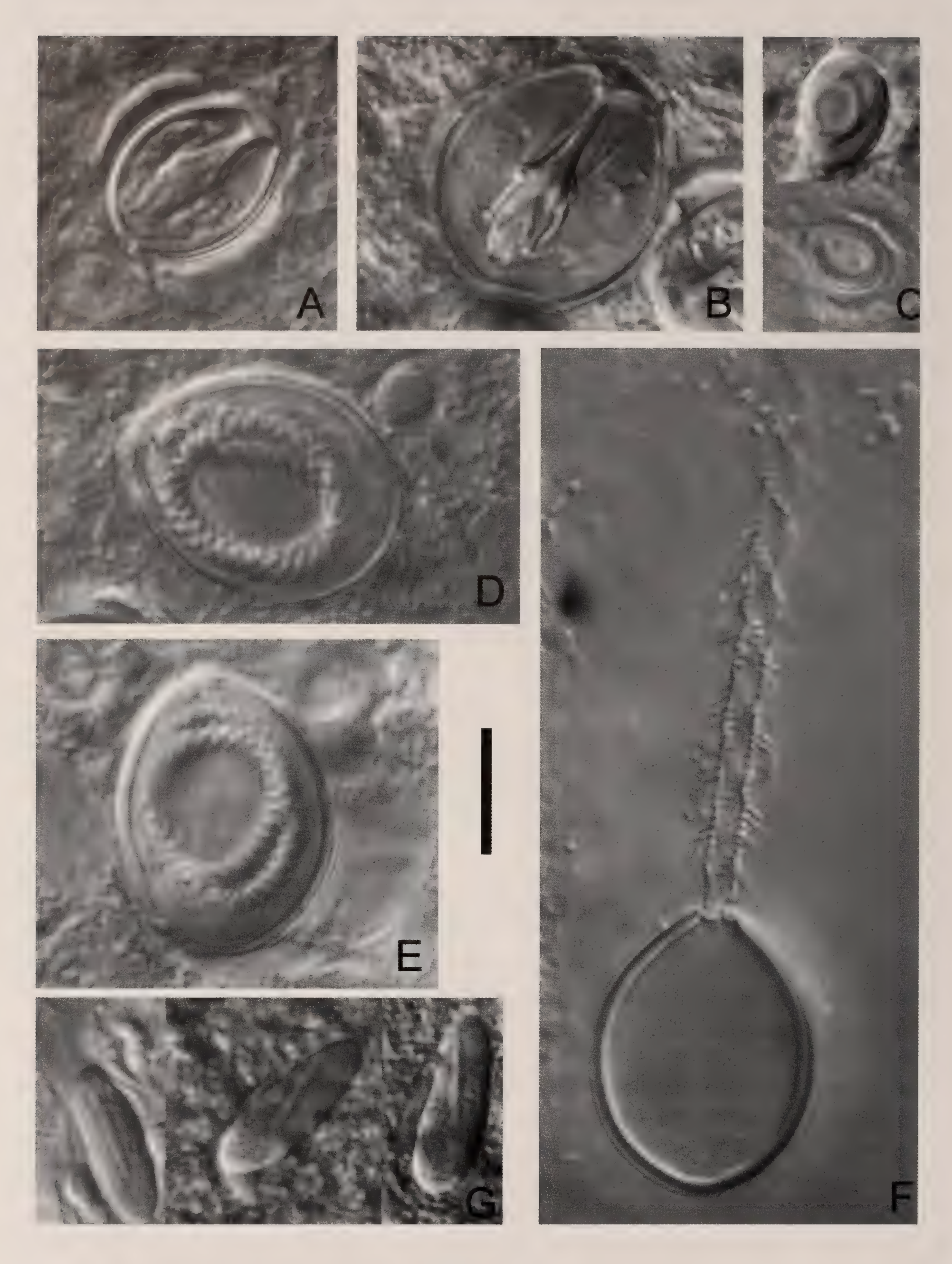


FIG. 22

Corymorpha glacialis M. Sars, 1860; alcohol-preserved nematocysts of deep water form from the Faroe-Shetland Channel (MHNG INVE 67049); scale bar 10 μm. (A) Small stenotele. (B) Large stenotele. (C) Desmonemes. (D-E) Undischarged heterotrichous anisorhizas. (F) Discharged anisorhiza, only proximal part of filament is visible. (G) Unidentified capsule, likely a heteroneme.



FIG. 23

Corymorpha glacialis M. Sars, 1860, living animal, MHNG INVE 67049; height of animal about 14 cm. Photo courtesy Daniel Jones, National Oceanography Centre, Southampton, SERPENT Project www.serpentproject.com.

Corymorpha groenlandica seems to lack the round haploneme usually present in other *Corymorpha* species (Fig. 22D-F). The gonophores of *Corymorpha sarsii* are fully formed medusae lacking only tentacles, allowing thus a more or less reliable identification of reproductive animals (see also diagnoses and key for these species). Moreover, the blastostyles of *C. glacialis* are almost always unbranched (Figs 19C, 21B), while those of *C. sarsii* are branched (Fig. 17A). As for most other athecate hydroids, non-reproductive material is almost impossible to identify reliably.

The two specimens from deep waters of the Faroe-Shetland Channel (INVE 67049-67050) posed some identification problems as they differed from material of more shallow waters. Besides being considerably larger and having more tentacles, it was especially the unusual shape of the hydranth which made me hesitate to allocate them to *C. glacialis*. When seen from the aboral side, the outline of the hydranth body is clearly kidney-shaped (Fig. 21A). Through the embayment on one side, the stem attachment lies rather close to the margin of the hydranth body. The situation is very much reminiscent of the genus *Branchiocerianthus*. In the larger female animal, some tentacles in the embayment zone are additionally missing – likely lost –, which adds to the impression that the animals belong to the genus *Branchiocerianthus*. Other diagnostic traits of the latter genus, however, are missing: the blastostyles are arranged in a circle and not in a horse-shoe shape, the hypostome is not excentric, the blastostyles are almost exclusively unbranched, and in the other, male specimen, the aboral tentacles were in a perfect whorl (not smaller or reduced at the site of the embayment) (compare Figs 21A, 30B, 33). I think that the reniform outline of the hydranth body is correlated to the much larger size of these animals. In life (Fig. 23), the hydranth body and the aboral tentacles are held almost vertical to the stem. This bending of the neck-region brings one side of the hydranth body and its tentacles close to the stem. It could be that this contact induces the reniform outline of the hydranth body and the loss of a few tentacles. Despite the differences, the two specimens were allocated to *C. glacialis*, although I admit that they could belong to a separate, undescribed species.

Corymorpha groenlandica (Allman, 1876) Figs 24-26

Monocaulus groenlandica Allman, 1876: 257, pl. 9 figs 7-8. – Svoboda & Stepanjants, 2001: 66, figs 2a-b.

Lampra purpurea Bonnevie, 1898: 478. – Bonnevie, 1899: 21, pl. 3 fig. 1. – Broch, 1916: 33, synonym. – Svoboda & Stepanjants, 2001: 67, fig. 1b: 3, 4.

Lampra atlantica Bonnevie, 1898: 479. – Bonnevie, 1899: 21, pl. 2 fig. 4. – Broch, 1916: 33, synonym. – Svoboda & Stepanjants, 2001: 67, fig. 1b: 1, 2.

? *Lampra sarsii* Bonnevie, 1898: 478, pl 26, fig. 21. – Bonnevie, 1899: 18, pl. 2 fig. 3a-ci. – Svoboda & Stepanjants 2001: 67, fig. 1b: 5, synonym. [not *Corymorpha sarsii* Steenstrup, 1855]

Lampra socia Swenander, 1904: 6, pl. figs 1-3. – Broch, 1916: 36, synonym.

Lampra arctica Jäderholm, 1907: 371. – Jäderholm, 1909: 41, pl. 1 fig. 9-10. – Broch, 1916: 33, synonym.

Corymorpha Spitsbergensis Broch, 1910: 140, fig 2. – Broch, 1916: 36, synonym.

? *Corymorpha abyssalis* Broch, 1910: 196, new name for *L. sarsii*. – Vervoort, 2009: 762.

Lampra socia. – Stechow, 1912b: 341, pl. 13 fig. 6.

Corymorpha groenlandica. – Broch, 1915: 11, pl. 4 figs 16-19. – Broch, 1916: 33, fig. I, pl. 2 figs 14-15. – Naumov, 1969: 232, fig. 101. – Calder, 1972: 220, pl. 1 fig. 2. – Schuchert, 2001a: 38, fig. 26A-B. – Vervoort, 2009: 766.

Material examined: MHNG INVE 33557; The Faroe Islands, 61.16°N 5.75°W, 246 m depth, collected 21.07.1989 for BIOFAR project, one large, fertile specimen with long, unbranched blastostyles. – MHNG INVE 63302; Faroe-Shetland Channel, 061.140889°N 003.67234°W, depth 1186 m; collected 27.02.2009 by David Jones (National Oceanography Centre, Southampton) by ROV, bottom with heterogeneous sediment characteristic of past ice rafting - grain size from boulders to clay; one well preserved reproductive female; one tentacle used to make DNA; 16S sequence accession number **FN687550**. – MHNG INVE 67051; West of Shetland, south Uist, 61.26686°N 02.9968488°W, 1157 m, collected 07.08.2009 by Daniel Jones; small, infertile animals, typical brick-red colour of *C. groenlandica*; 16S sequence **FN687551**.

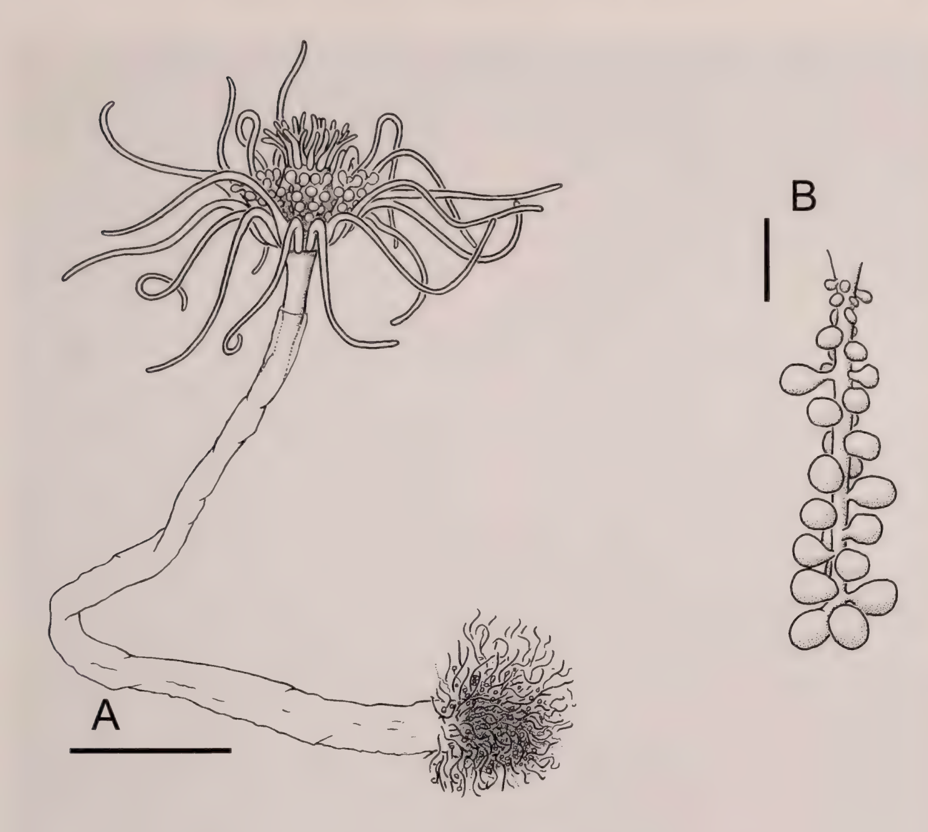


FIG. 24

Corymorpha groenlandica (Allman, 1876). (A) Preserved, nearly mature animal. Note that in living or very well preserved animals the upper limit of the perisarc is not visible (comp. Fig. 25) ; scale bar 1 cm. (B) Blastostyle of mature animal; scale bar 2 mm.

DIAGNOSIS: *Corymorpha* polyp 1.5-10 cm, preserved material reddish-brown, gonophores round, sporosacs without any radial canals, growing evenly distributed on long, unbranched blastostyles.

DESCRIPTION: Solitary hydroids, with long caulus (stem), well demarcated from hydranth body, increasing in diameter towards basal end, covered by filmy perisarc (visible in shrunken, preserved animals only). Visible perisarc in preserved and shrunken animals ends below upper end of caulus and thus delimits a distal neck region of the caulus. Coenosarc of stem with 14-18 longitudinal canals, with anastomoses. Basal end with numerous tangled, thin attachment filaments.

Hydranth body broadly flask-shaped, aboral whorl of 10-35 rather thin tentacles, bases continued as ridges on hydranth body almost to attachment site of stem, oral tentacles rather short, up to 80 in number, in 2-4 closely set whorls, innermost tentacles small, outer ones longer.

Gonophores arise from 8-32 blastostyles developing just above aboral tentacles. Blastostyles very contractile, simply rod-shaped and not branched, bearing many even-

ly distributed gonophores, with a gradient of developmental stages from mere buds proximally to fully developed at distal end.

Gonophores usually spherical to oval, sporosacs without traces of radial canals, circular canal, or tentacles. Females with about 10-12 eggs, female sporosacs reportedly somewhat larger and rounder than male ones.

Colours: living animals pale rust-coloured to purple-reddish, sporosacs white. In preservative (formalin), the tissues including the sporosacs get much darker after some months, resulting in characteristic orange-brown to purple-brown coloured specimens.

Nematocysts: stenoteles, desmonemes, and characteristic, large, almond-shaped microbasic mastigophores.

Variation: *Corymorpha groenlandica* seems to continue its growth even after the onset of gonophore production. This results in animals that differ significantly in size and numbers of tentacles.

Dimensions: Height of polyp when mature 1.5-10 cm, in life perhaps even larger when fully expanded. Stem diameter up to 2-3 mm. Sporosacs about 1 mm in diameter. The aboral tentacles and the blastostyles when extended can attain a length of 4 cm, oral tentacles 9 mm (Broch, 1916). Nematocysts (alcohol preserved material): larger stenoteles (15-16.5)x(11-12.5)μm, smaller stenoteles (13-14.5)x(10.5)μm, desmonemes (7.5)x(6-6.5)μm, almond-shaped microbasic mastigophores (16-17.5)x(8.5-9.5)μm.

Biology: *Corymorpha groenlandica* is a typical cold- and deep water species. It has been recorded from 36 to more than 2000 m depth, mostly below 300 m. The eggs develop within the sporosac. Asexual multiplication of the polyp via frustules has been observed by Antsulevich & Polteva (1988).

Distribution: Widespread in the Arctic, in deep waters occurring as far south as the Faroe-Shetland Channel, perhaps the most common deep-sea *Corymorpha* species of the region. Recorded from Greenland (west coast to Cape Farewell), Iceland, Spitzbergen, Faroe and Shetland Islands Islands, northern Norway, Barents Sea, Laptev Sea, Beaufort Sea, Kuriles (Bonnevie, 1899; Broch, 1916; Calder, 1972; Antsulevich & Polteva, 1988; Schuchert, 2001a; Svoboda & Stepanjants, 2001; Vervoort, 2009).

Remarks: Preserved *Corymorpha groenlandica* specimens are rather conspicuous due to their orange-brown to purple-brown colour. Living animals are much paler to almost colourless (Fig. 25; Svoboda & Stepanjants, 2001: fig. 2a), but the colour gets darker after a few months in preservative (own observation MHNG INVE 63302; Svoboda & Stepanjants, 2001) and hardly fades after many years (Naumov, 1969). The colour of preserved animals is a helpful diagnostic feature of the species which makes it easily distinguishable from polyps with a similar trophosome like *C. nutans* and *C. glacialis*. Additionally, also the large, almond-shaped mastigophore (Fig. 26D-H) is a useful character to identify the species, although it is not known whether this is a diagnostic trait for the *Corymorpha* of the region. The capsule is a somewhat atypical mastigophore as the shaft tapers towards distal (Fig. 26G). It could also be regarded as an atypical anisorhiza.

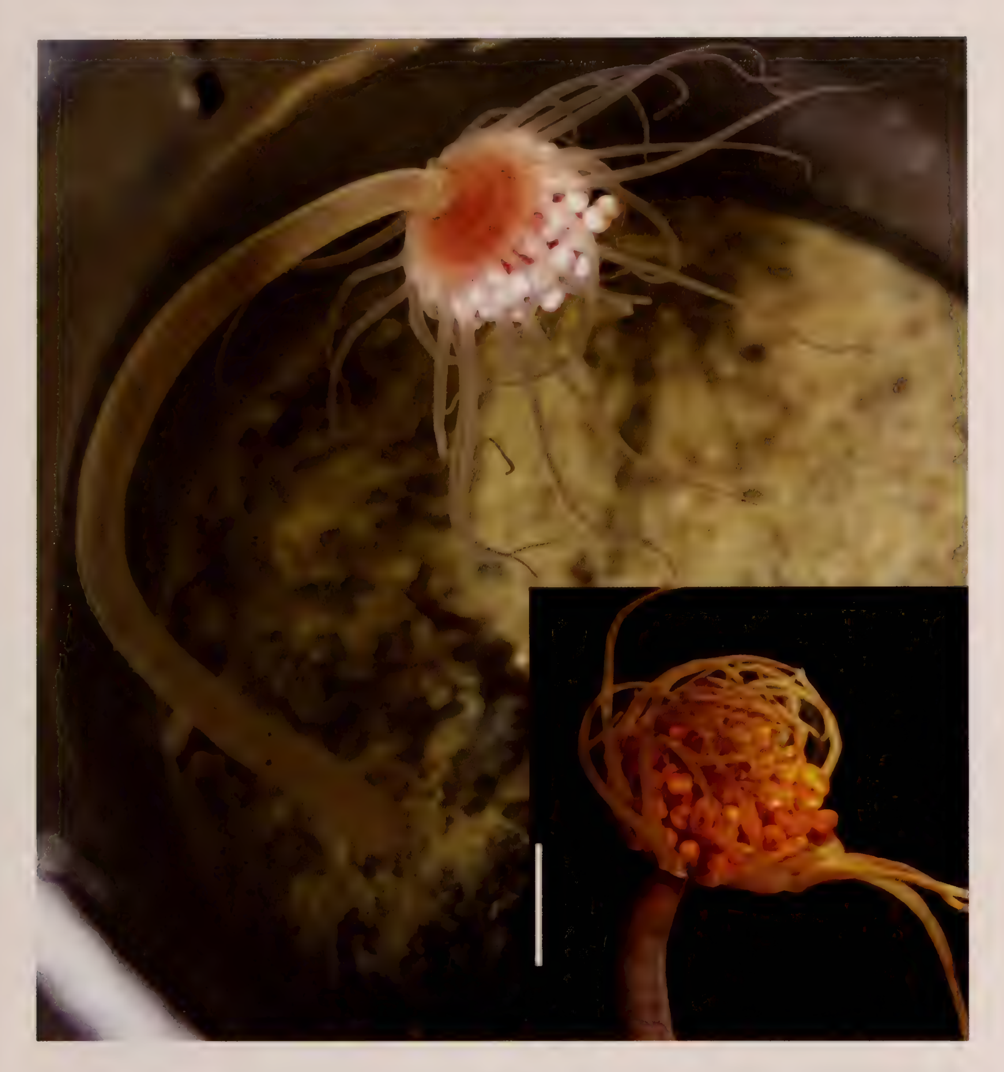


FIG. 25

Corymorpha groenlandica (Allman, 1876), living animal immediately after capture, note rather pale colour. The colour get much darker after having been in the preservative for a few months. Photo courtesy of Dr David Jones (National Oceanography Centre, Southampton). Inset, same animal after a few months in formalin fixative, scale bar 5 mm.

Broch (1916) and Svoboda & Stepanjants (2001) revised the numerous *Corymorpha* species known from the north Atlantic and put forward good arguments that a number of nominal species are actually conspecific with *C. groenlandica*. These species differ mainly in the number of tentacles, number of blastostyles and size, traits that are rather unsuitable to discriminate different species.

Calder (1972) thinks that *Rhizonema carnea* Clark, 1877 from Alaska is possibly conspecific with *C. groenlandica*, which seems plausible. The colour of Clark's specimens were "coral-red", thus approaching *C. groenlandica*. Clarke (1903)

redescribed his material, although he did not use the name *Rhizonema carnea* again. The clustered gonophores of Clarke's figures suggest that the two nominal species might nevertheless be separable. Unfortunately, Clarke could not describe the nature of the gonophores. For a well founded decision more material from Alaska must be examined. The Japanese material described by Stechow (1909a: 47) and Hirohito (1988) as *C. carnea* produces medusae with a single tentacle and is thus clearly distinct from *C. groenlandica* and most likely also *C. carnea*.

Bonnevie (1898, 1899) described *Lampra sarsii* based on material from northern Norway. It is very similar to *C. groenlandica* in almost all details, differing only in sporosacs with a single tentacle. The sporosacs were depicted in detail by Bonnevie (1899). Because the hydrozoan genus *Lampra* is invalid and because he synonymized it with *Corymorpha*, Broch (1910) suggested the new name *C. abyssalis* to avoid the secondary homonymy with *C. sarsii* Steenstrup, 1855. Svoboda & Stepanjants (2001) re-examined Bonnevie's type material and referred it to *C. groenlandica*. Vervoort (2009) disagreed with this and maintains it as distinct species (*C. abyssalis*) because of the tentacle on the sporosac. Its status is thus not entirely clear. A similar intraspecific variation with rare mono-tentaculate gonophores is also seen in the closely related species *C. sarsii* (see Sars, 1877: 8, pl. 6 fig. 12). Also *T. indivisa* shows the same variability.

Corymorpha bigelowi (Maas, 1905)

? *Euphysa tetrabrachia* Bigelow, 1904: 251, pl. 1 fig. 1. – Mayer, 1910: 37, questionable synonym.
Euphysora bigelowi Maas, 1905: 7, pl. 1 figs 1-3. – Kramp, 1961: 39. – Kramp, 1968: 14, fig. 26. – Bouillon, 1978b: 262. – Bouillon *et al.*, 2004: 92, fig. 49H-I.
Steenstrupia bigelowi. – Mayer, 1910: 36, fig. 9.
Euphysa bigelowi. – Uchida, 1927: 189, fig. 28, pl. 10 fig. 3.
Corymorpha bigelowi. – Petersen, 1990: figs 16C, 17a. – Sassamann & Rees, 1978: 485, figs 1-3. – Vervoort, 2009: 763.

DIAGNOSIS: Medusa up to 5 mm high, with pointed apical process, with or without remnants of an apical canal; principle tentacle long, with several large nematocyst knobs in a unilateral, adaxial position and a distinct terminal knob, the three other perradial bulbs each with a short, pointed tentacle without nematocyst clusters.

Polyp typical for genus, 13 mm up to high, few gastrodermal canals (about 3), 15-20 aboral tentacles number, up to 35 oral tentacles in irregular whorls, medusa buds on blastostyles (Sassaman & Rees, 1978).

OTHER DATA: For nematocysts measurements see Bouillon (1978b)

DISTRIBUTION: Scattered records in the Indo-Pacific Ocean, mostly in tropical waters (Kramp, 1961; Vervoort, 2009). Perhaps also eastern Mediterranean (Schmidt, 1973b). Type locality: Maas's material came from several localities of the Malayan Archipelago.

REMARKS: This species does not occur in European waters. The presence of this species in the ERMS zone is solely based on an uncommented record of two preserved medusae along the coast of Israel (Schmidt, 1973b). Without any figure or description, the identification lacks some credibility. The presence of *E. bigelowi* in the Mediterranean is thus somewhat doubtful and needs further confirmation by more findings and also life-cycle observations.

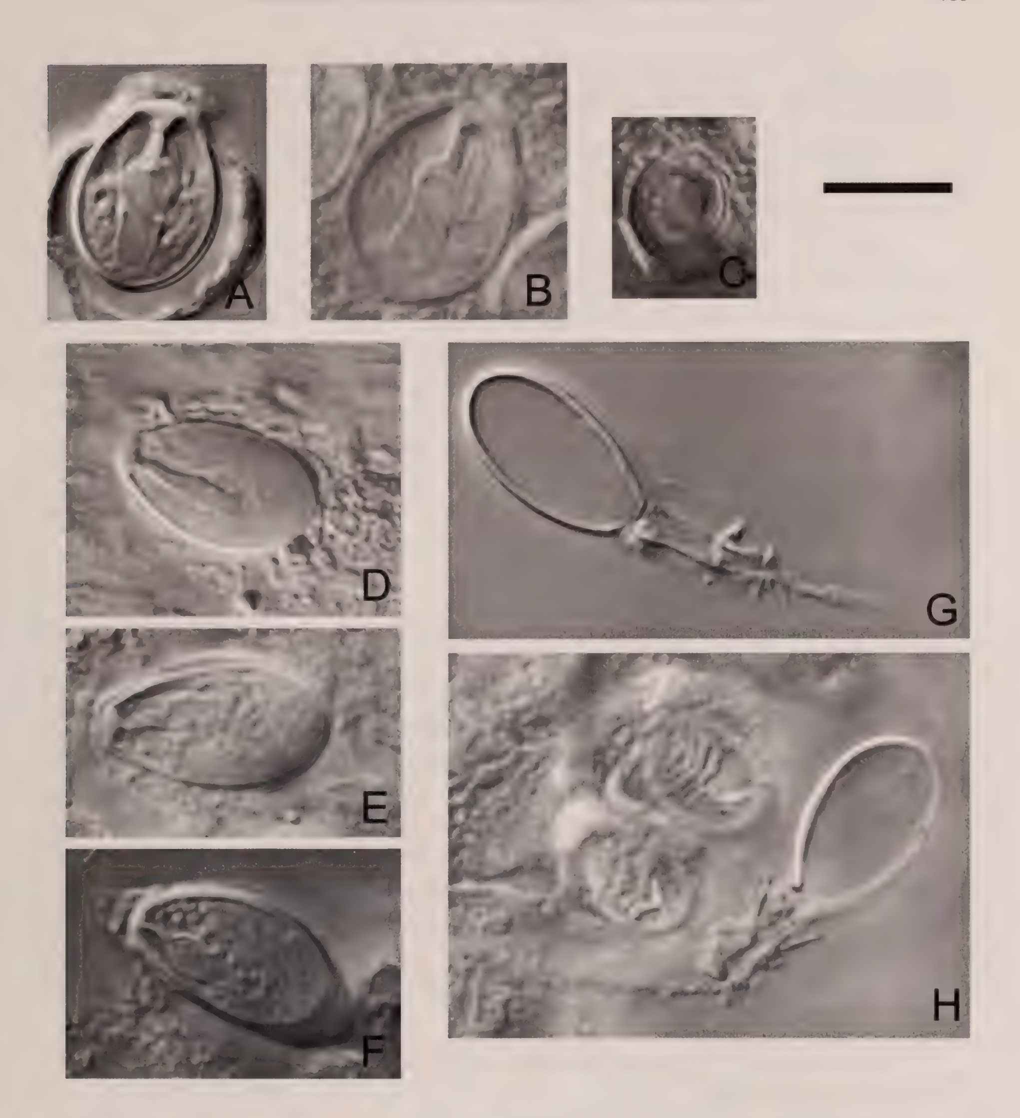


FIG. 26

Corymorpha groenlandica (Allman, 1876); nematocysts after preserved material (MHNG INVE 33557 and 63302); scale bar 10 μm. (A) Smaller type of stenotele. (B) Larger stenotele. (C) Desmoneme. (D-F) Microbasic mastigophores, intact capsule. (G-H) Microbasic mastigophore, discharged capsule.

Corymorpha annulata (Kramp, 1928)

Euphysora annulata Kramp, 1928: 39, fig. 13. – Kramp, 1961: 39. – Kramp, 1968: 14, fig. 27. – Schmidt & Benovic, 1977: 636. – Schmidt & Benovic, 1979: 195. – Bouillon *et al.*, 2004: 91, fig. 49G.

DIAGNOSIS: *Corymorpha* medusa 2 mm high and 1.4 mm wide, barrel-shaped, with thin walls and a pointed apex with an apical canal; manubrium as long as bell cavity. One long tentacle and three short tentacles. Long tentacle moniliform, with

numerous rings of nematocysts, three other tentacles short, cone-shaped, with the one opposite the main tentacle longer than the two others. Polyp unknown.

DISTRIBUTION: Sunda Strait, northeastern Australia, Madras in India, Red Sea (Kramp, 1968; Schmidt, 1973a), and perhaps Adriatic Sea (Schmidt & Benovic, 1977). Type locality: Sunda Strait, near water surface.

REMARKS: The presence of *C. annulata* in the Mediterranean and the ERMS zone is based on the report of Schmidt & Benovic (1977, 1979), who found a single medusa in the Adriatic Sea. *Corymorpha annulata* resembles *C. nutans*, except that the three otherwise atentaculate bulbs bear rudimentary tentacles. *Corymorpha nutans* has usually no tentacles on these three bulbs, but Neppi & Stiasny (1913, as *S. rubra*) observed that the atentaculate bulbs of Mediterranean *C. nutans* may rarely have rudimentary tentacles. This would render them formally indistinguishable from *C. annulata*. It is possible that Schmidt & Benovic (1977) had in fact such an aberrant specimen of *C. nutans*. More observations are needed to confirm the Mediterranean presence of rare Indo-Pacific medusa *C. annulata*.

Genus ***Gymnogonos*** Bonnevie, 1898

Gymnogonos Bonnevie, 1898; type species *Gymnogonos crassicornis* Bonnevie, 1898 by monotypy.

DIAGNOSIS: Hydroid with stout caulus, almost as thick as the hydranth, covered by membranous perisarc originating just under aboral tentacles, gastrodermis parenchymatic and with central lumen, peripheral longitudinal canals may be present in lower third; exterior papillae immediately under hydranth; with rooting filaments at aboral end of caulus, these with gastrodermal statocysts. Hydranth not clearly separated from stem, usually demarcated from stem by annular furrow, furrow may be absent; one to three whorls of moniliform or pseudofiliform oral tentacles and one whorl of longer moniliform or filiform aboral tentacles. Gastric cavity without gastrodermal diaphragm. Gonophores are fixed sporosacs on short pedicels developing directly on hydranth over aboral tentacles or on very short, stubby blastostyles, branched blastostyles absent.

REMARKS: All *Gymnogonos* species have been reviewed recently by Stepanjants & Svoboda (2001, 2008).

KEY TO SPECIES OF *GYMNOGONOS* OF THE ERMS ZONE:

1a size up to 17 mm, with circular furrow below tentacles, with rooting filamants . . . . *G. crassicornis*

1b size up to 32 mm, no furrow below tentacles, without rooting filamants . . . . *G. obvolutus*

Gymnogonos crassicornis Bonnevie, 1898 Fig. 27

Gymnogonos crassicornis Bonnevie, 1898: 481, pl. 25 figs 1-4, 5-11. – Kramp, 1949: 200, fig. 8. – Schuchert, 2001a: 41, fig. 28A-B. – Stepanjants & Svoboda, 2001: 250. – Stepanjants & Svoboda, 2008: 1620, figs 1A–F, 5.

Gymnogonos crassicaulis. – Schuchert, 2001a: 41. [incorrect subsequent spelling]

MATERIAL EXAMINED: Icelandic Museum of Natural History, BIOICE 2233; Iceland, 63.71°°N 24.41°W, 209 m, collected 04.09.1992; one fertile animal (Schuchert, 2001a). – Polish

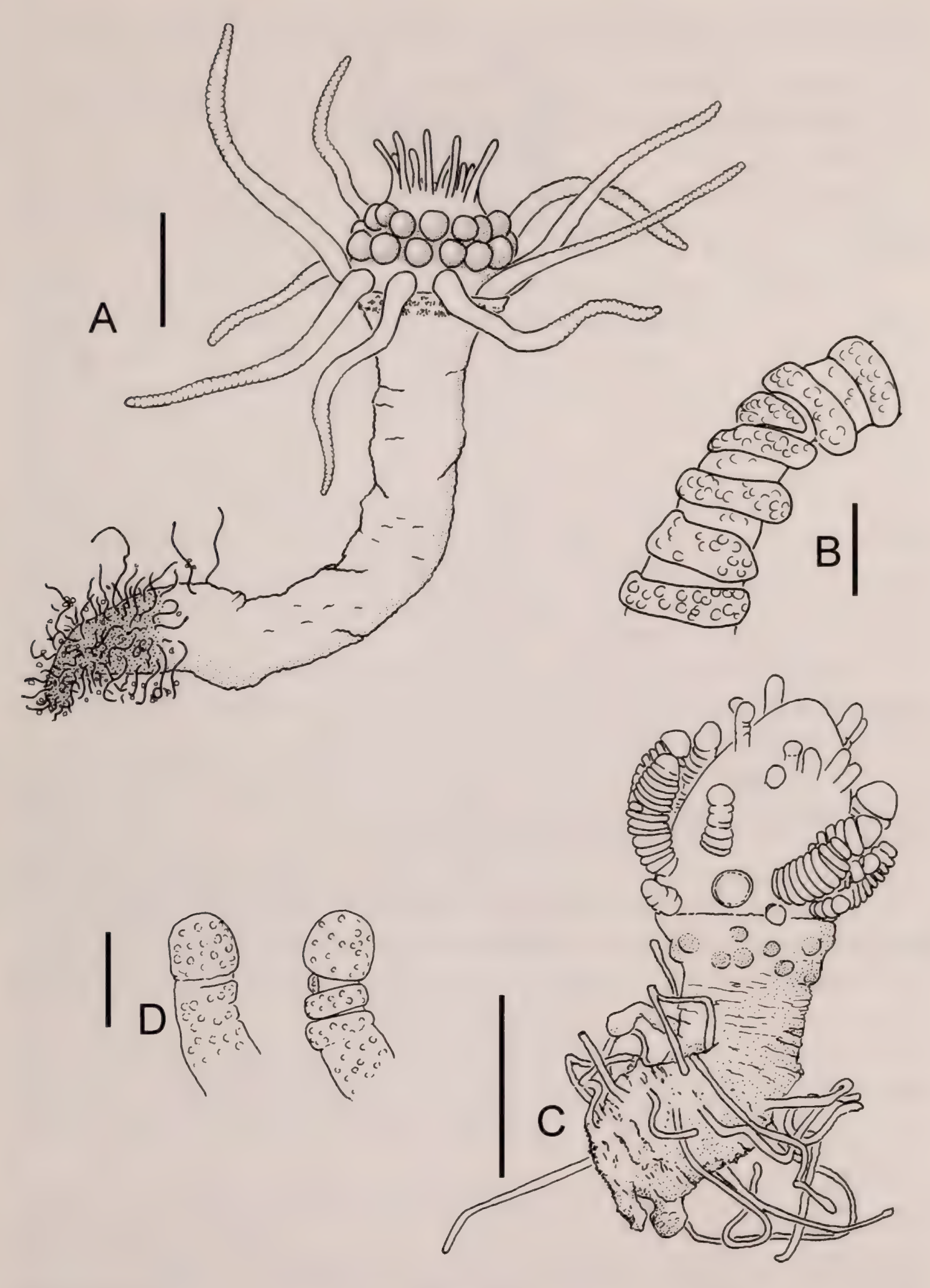


FIG. 27

Gymnogonos crassicornis Bonnevie, 1898; schematized after preserved material. (A) Reproductive polyp from Iceland, not all rooting filaments shown, scale bar 1 mm. (B) Part of aboral tentacles of animal shown in A, note moniliform arrangement of nematocyst clusters, scale bar 0.2 mm. (C) Juvenile animal from Spitzbergen, scale bar 1 mm. (D) Tips of oral tentacles of animal shown in D with a tendency of nematocyst clustering, scale bar 0.2 mm.

Academy of Sciences, Institute of Oceanology; Svalbard Archipelago, north Spitzbergen, depth 13 m, collected 23.09.2001; two juvenile specimens.

DIAGNOSIS: *Gymnogonos* species reaching 17 mm in size, with circular furrow below aboral tentacles, with rooting filaments, sporosacs solitary, in two circles or a broad band.

DESCRIPTION (after own data and Stepanjants & Svoboda, 2008): Solitary hydroid, with thick, conical caulus intergrading directly into hydranth without forming neck region, caulus demarcated from hydranth by a circular furrow.

Caulus bent, broadest below hydranth, then tapering and again slightly swollen at lower end, covered by filmy perisarc, perisarc terminates just below aboral tentacles, lower end darker due to adhering sediment particles, this region also with numerous, entangled rooting filaments. Rooting filaments end in small statocyst-like vesicles. Below furrow separating caulus from hydranth a belt with distinct papillae in about three transverse rings.

Hydranth body broadly conical, with one whorl of aboral tentacles and two closely set whorls of oral tentacles around mouth. Aboral tentacles up to 13 in number, hollow, oval in cross-section, with nematocysts concentrated in somewhat indistinct annular thickenings (moniliform). Oral tentacles about 20 in number, much shorter than aboral ones, of variable length, some with indistinct terminal swelling, in juveniles indistinctly moniliform.

Gonophores sessile sporosacs, spherical, about 30 in two circles or a broad band between oral and aboral tentacles, attached directly to hydranth body by thin pedicel, without radial canals or circular canal, no bulbs, no velum.

Nematocysts: stenoteles, desmonemes, ? mastigophores (= rhabdoids).

DIMENSIONS: Height of fertile polyps 5-17 mm, up to 3 mm infertile. Nematocyst sizes see Stepanjants & Svoboda (2001, 2008).

OTHER DATA: As in *Euphysa* polyps, there is no diaphragm separating the gastric cavity of the hydranth from the lumen of the caulus as seen in *Corymorpha* or *Branchiocerianthus* (Bonnevie, 1898; Petersen, 1990; Stepanjants & Svoboda, 2008).

BIOLOGY: A very rare species living like other corymorphids partially embedded in sediment; the known depth range is from 13 to 400 m.

DISTRIBUTION: A high boreal-Arctic species, recorded from mid-Norway (Bonnevie, 1898), Iceland (Schuchert, 2001a), Barents Sea (Stepanjants & Svoboda, 2001), and Svalbard (this study). Type locality: near Beian, Trondheimsfjord, Norway, 400 m.

REMARKS: Stepanjants & Svoboda (2008) state that contrary to *G. obvolutus*, there are no peripheral canals in the stem of *G. crassicornis*. No such canals could be seen from the outside of the material examined here, but their absence cannot be confirmed with certainty. The diagnosis of the genus of Petersen (1990) was therefore modified with respect to this matter.

Gymnogonos obvolutus (Kramp, 1933) Fig. 28

Corymorpha obvoluta Kramp, 1933: 4, figs 1-9.
Heteractis obvoluta. – Kramp, 1949: 194, fig. 5.

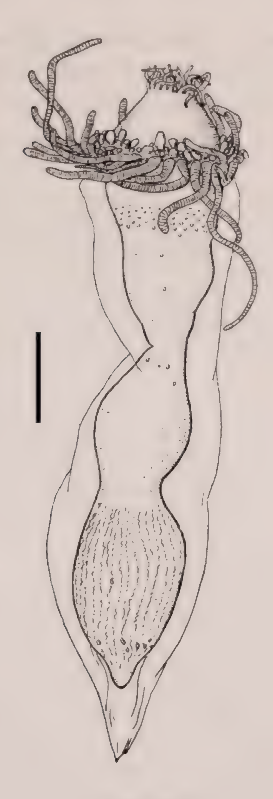


FIG. 28
Gymnogonos obvolutus (Kramp, 1933); type specimen, scale bar 0.5 cm, from Kramp (1933a).

Gymnogonos obvolutus. – Petersen, 1990: 148, fig. 16A. – Schuchert, 2001a: 42. – Stepanjants & Svoboda, 2001: 250. – Stepanjants & Svoboda, 2008: 1620, Figs 2A–G, 5.

DIAGNOSIS: *Gymnogonos* species reaching 32 mm in size, without circular furrow below aboral tentacles, without rooting filaments, sporosacs oblong and in clusters of 3-5, in one circle or narrow band.

DESCRIPTION (Kramp, 1933; Stepanjants & Svoboda, 2008): Solitary hydroid, with thick, conical caulus intergrading directly into hydranth without forming neck region, caulus not demarcated from hydranth by a circular furrow.

Caulus broadest below hydranth, then tapering and again slightly swollen at lower end, covered by gelatinous perisarc, perisarc terminates just below aboral tentacles. Rooting filaments absent. Below aboral tentacles a belt with distinct papillae in several transverse rings.

Hydranth body broadly conical, with one whorl of aboral tentacles and one whorl of oral tentacles around mouth. Aboral tentacles up to 28 in number, hollow, with nematocysts concentrated in annular thickenings (moniliform). Oral tentacles about 20 in number, much shorter than aboral ones.

Gonophores in a circle immediately above aboral tentacles, in clusters of 3-5, with thin pedicels, attached to hydranth body via a short, bump-like blastostyle.

Gonophores are cryptomedusoids, elongate-oval, with four small terminal knobs containing nematocysts, in young sporosacs primordia of radial canals in distal region, later lost.

Nematocysts (Stepanjants & Svoboda, 2001): stenoteles, desmonemes and ? mastigophores (rhabdoids).

DIMENSIONS: Polyp reaches sizes of at least 32 mm and 6 mm diameter, reproductive also at smaller sizes. Sporosacs approximately 1 mm. Nematocyst sizes, see Stepanjants & Svoboda (2001, 2008).

BIOLOGY: A very rare species living like other corymorphids partially embedded in sediment; the known depth range is from 10 to 175 m (Stepanjants & Svoboda, 2008).

DISTRIBUTION: Arctic, so far recorded from southeast Greenland (Kramp, 1933), in the Laptev Sea, and the East Siberian Sea (Stepanjants & Svoboda, 2008). Type locality: Kangerlussuaq, south-eastern Greenland (68.33°N 32.33°W), 175 m, muddy botton.

Genus ***Branchiocerianthus*** Mark, 1898

Branchiocerianthus Mark, 1898; type species *Branchiocerianthus urceolus* Mark, 1898 by monotypy.

Branchiaria Stechow, 1921b; type species *Branchiaria mirabilis* Stechow, 1921b by monotypy,

DIAGNOSIS: Very large, bilaterally symmetric corymorphid hydroids; hydrocaulus long and relatively thin, perisarc rudimentary, basal end with rooting filaments, interior filled with parenchymatic endoderm, with longitudinal peripheral canals. Hydranth bilaterally symmetrical and joined excentrically to hydrocaulus, hypostome also displaced away from centre of hydranth; several whorls of filiform oral tentacles and one whorl of filiform aboral tentacles, aboral tentacles shorter near attachment site of caulus; thin diaphragm dividing gastric cavity into oral and aboral chamber; with radial canals leading from oral chamber to hollow blastostyles continued to margin of hydranth, ending blindly between aboral tentacles. Gonophores arise on blastostyles developing immediately above aboral tentacles, blastostyle-arrangement U-shaped, opening of U directed towards attachment site of caulus. Mature gonophores unknown.

REMARKS: The large size of some *Branchiocerianthus* species – some reportedly reach heights of more than 2 m – makes them indeed exceptional among all hydroids. They all occur in deep or very deep waters and only few, mostly badly preserved, specimens are known. This is certainly the main reason why they remain imperfectly known, notably their gonophores and reproduction. Currently, six nominal species are recognized (Bouillon *et al.*, 2006). It is not clear whether these names represent true biological species or if some of them are synonyms. Allman (1885, 1888) described the first and largest specimens collected by the Challenger expedition near Japan and in the North Pacific as *Monocaulus imperator*. The bad state of preservation did not make it evident that they differ from other Corymorphidae by their bilaterally symmetric hydranth. The second species, *B. urceolus* Mark, 1898 from the Pacific coast of Panama, was initially mistaken for a species of Cerianthidae (Anthozoa) with gills, hence its genus name *Branchiocerianthus*. The species does not

differ much from *B. imperator*. Apart from its smaller size (20 cm), the only difference is the more excentric attachment of its stem (Stechow, 1909a) and perhaps also the branching radial canals (Fig. 30). Broch (1918) then introduced the name *B. reniformis* for a single, much damaged specimen from western Greenland. It was also smaller than *B. imperator* and the hydranth had a kidney-shaped contour. This shape could be a fixation artefact as I have seen the same in a *B. imperator* specimen from Japan. Stechow (1921b) then introduced the name *B. italicus* for a Mediterranean *Branchiocerianthus* specimen mentioned by Lo Bianco (1909), however without giving any useful diagnostic traits. In the same paper, Stechow (1921b) also referred some smaller Japanese specimen of *B. imperator* which he had previously described (1909a) to a separate species named *Branchiaria mirabilis*. Stechow introduced the new genus name in order to emphasize the difference from *B. imperator*: the branched radial canals and the lack of nematocyst clusters on the blastostyles. In his earlier studies, he had interpreted these traits as being due to the juvenile stage of the specimens. The type species of *Branchiocerianthus*, *B. urceolus*, also has branched radial canals (Mark, 1898: 150), which renders *Branchiaria* de facto congeneric with *Branchiocerianthus*. I therefore concur with Vervoort (1966) that *Branchiaria* Stechow, 1921b must be regarded as a synonym of *Branchiocerianthus*. The most recently described *Branchiocerianthus* species is *B. norvegicus*. Brattström (1957) described the single specimen with great detail and compared it to the other known species. The species remain difficult to separate and Brattström (1957) recommends using the shape of the hydranth or the oral disk (= upper surface of hydranth) as a diagnostic feature: more or less circular outline of the oral disk in *B. imperator*, reniform outline in *B. reniformis*, ovoid outline in *B. norvegicus*, and a vase-shaped hydranth in *B. urceolus*. *Branchiocerianthus imperator* produces the largest polyps (23-224 cm) while the others remain smaller (10-24 cm). In a subsequent paper, Brattström (1972) reported upon a second specimen of *B. norvegicus* with a circular hydranth, whereby invalidating this character to discriminate the species. I suspect that at least *B. reniformis*, *B. italicus*, and *B. norvegicus* belong to the same species.

The gonophores of all *Branchiocerianthus* species remain unknown, despite the genus diagnosis given by most recent authors purport that they are fixed sporosacs (e. g. Millard, 1975; Petersen, 1990; Bouillon *et al.*, 2006). However, all so far described *Branchiocerianthus* specimens with developed blastostyles and also those available for examination to me had only gonophores that were in the earliest stages of development, being nothing more than mere buds with a few cells (cf. Miyajima, 1900; Stechow, 1909a; Brattström, 1957). Although they were present in immense numbers, they appear to be arrested in their growth and their developmental stage does not allow making any conclusion relating to their final structure. Stechow (1909a: 61) acknowledges that only the putative gonophore buds are known, but he makes nevertheless an inadmissible assumption by stating "the immature gonophores lack features of a medusa, thus they will likely develop into sporosacs..." It could well be that the gonophores are medusoids or even free medusae and that some nominal species differ in respect to this. The paucity of reproductive animals can perhaps be explained by them being long-lived and their reproduction confined to very short periods.

Considering the imperfect knowledge we have, it seems currently advisable to retain all nominal species until new material permits better founded conclusions. The key presented below is thus certainly only provisional.

KEY TO SPECIES OF *BRANCHIOCERIANTHUS* of the North Atlantic and Mediterranean:

1a	stem > 20 cm, blastostyle with terminal nematocyst buttons	*B. imperator*
1b	stem < 20 cm, blastostyle without terminal nematocyst buttons	2
2a	hydranth oval or round in aboral view	3
2b	hydranth kidney shaped in aboral view	[*B. reniformis*]*
2a	in North Atlantic	*B. norvegicus*
2b	in Mediterranean	*B. italicus*

* known only outside the ERMS zone

Branchiocerianthus imperator (Allman, 1885) Figs 29-31

Monocaulus imperator Allman, 1885: 753, fig. 265. – Allman, 1888: 5, pl. 3 figs 1-7.
Branchiocerianthus imperator. – Miyajima, 1900: 235, pls 14-15. – Stechow, 1908b: 1, figs 1-6. – Stechow, 1909a: 49, figs 1-4, pl. 7 figs 1-8. – Stechow, 1909b: 296. – Stechow, 1913: 55. – Brattström, 1957: 5. – Vervoort, 1966: 99. – Millard, 1975: 28: fig. 13. – Omori & Vervoort, 1986: 257, figs 1-2.

MATERIAL EXAMINED: MHNG INVE 54660; Japan, Okinose, depth 730 m; collected 20.01.1904; leg. A. Owston; much-fragmented specimen preserved in alcohol, 10-20 cm, oral disk somewhat reniform, with blastostyles and tiny (70 μm) gonophore buds, blastostyles with nematocyst clusters.

DIAGNOSIS: *Branchiocerianthus* species measuring 23 to 224 cm in height, outline of hydranth circular or slightly oval, stem joining hydranth near its rim (very excentrical), radial canals of oral disk unbranched in adults, > 100 aboral tentacles, blastostyles branched, ending with nematocyst clusters.

DESCRIPTION (Miyajima, 1900; Stechow, 1909a; Millard, 1975): Stem and hydranth very large. Hydrocaulus tubular, narrowest distally and separated from hydranth by diaphragm and an annular constriction, widening basally and ending in a bulbous swelling bearing numerous tangled anchoring filaments. Base of hydrocaulus and anchoring filaments covered with thin, membranous perisarc. Stem filled with large, vacuolated gastrodermal cells, at periphery 15-20 longitudinal gastrodermal canals, visible from outside as longitudinal striation.

Hydranth disc-shaped to somewhat oval, bilaterally symmetrical, especially in younger individuals, with an excentric ("ventral") insertion of hydrocaulus and an excentric ("dorsal") hypostome; hydranth obliquely attached to hydrocaulus (ca 45°). Hypostome round in section. Aboral tentacles 100-250 in number, in one, or in two closely alternating whorls, the series broken in the ventral position where new tentacles develop, resulting in a length gradient of the aboral tentacles from "ventral" to "dorsal" side, aboral tentacles hollow at base, more distally filled with parenchymatic gastrodermis. Oral tentacles 48-180 in number in several close whorls. Internal cavity of hydranth divided by a transverse diaphragm with a circular opening at the level of tentacles. Many unbranched radial canals present immediately above diaphragm and ending blindly at periphery, alternating with tentacles and thus same in number.

Blastostyles 96-160 in number, in 1-3 whorls, the youngest and shortest "ventral", oldest ones branching 6-8 times or more, bearing in total up to 600 gono-



FIG. 29
Branchiocerianthus imperator (Allman, 1885); upper and lower end of polyp (total height 70 cm), note that the spherical appendages of the blastostyles are not gonophores but clusters of gonophores; modified after Miyajima (1900) and Millard (1975), scale bar 2 cm.

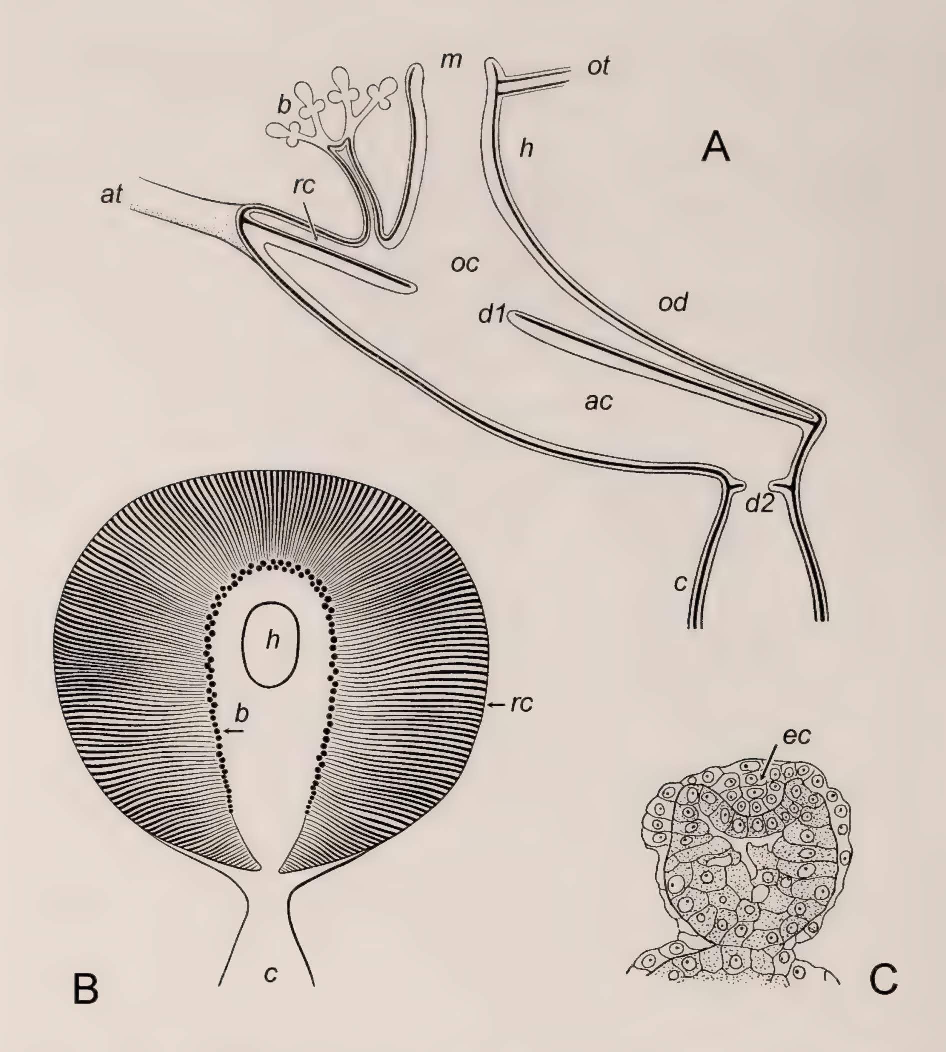


FIG. 30

Branchiocerianthus imperator (Allman, 1885); modified after Miyajima (1900). (A) Schematic organisation of the hydranth in a vertical section, in black mesogloea. (B) Schematic representation of the oral disk seen from above, tentacles removed. (C) Histological section of the most advanced gonophore buds found hitherto, size estimated 0.05 mm. Abbreviations: *ac* aboral gastric chamber, *at* aboral tentacle, *b* blastostyle, *c* caulus/stem, *d1* diaphragm separating preoral chamber from gastric cavity, *d2* diaphragm separating hydranth from caulus, *ec* entocodon, *h* hypostome, *m* mouth, *oc* oral chamber, *od* oral disk, *ot* oral tentacle, *rc* radial canal.

phore buds, mature gonophore unknown. Branches of blastostyle terminating in a single small globule with nematocysts. Colours: hydranth pink, tentacles dark red.

DIMENSIONS (Brattström, 1957): Total height from 23 to 224 cm, diameter of caulus 4-15 mm, length of hydranth 23-90 mm, width of hydranth 23-80 mm, length of aboral tentacles 48-180 mm, longest blastostyles 8-63 mm.

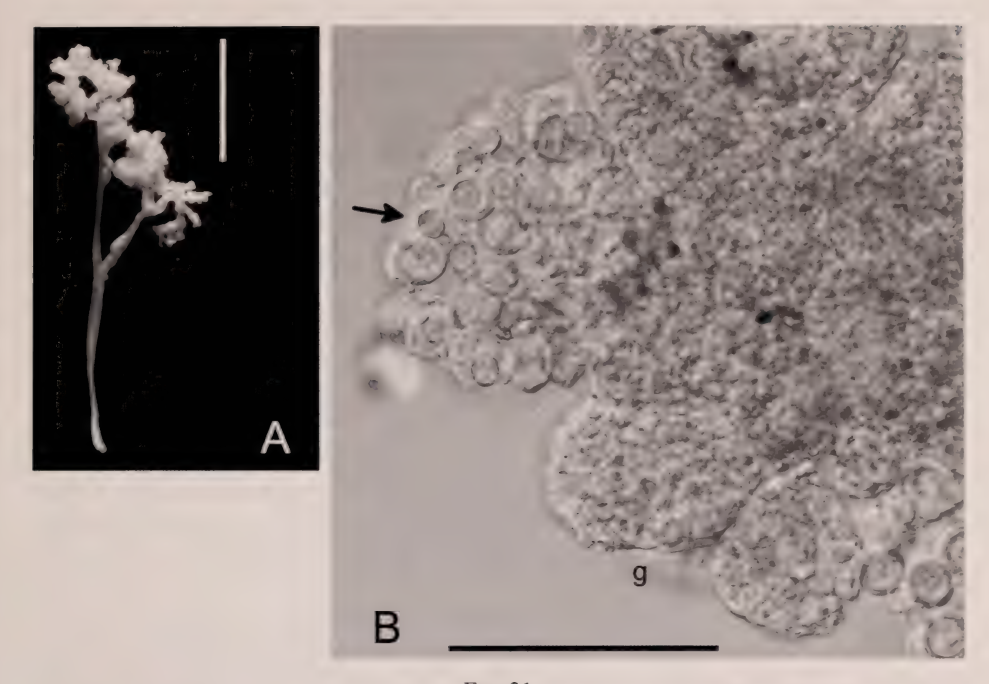


FIG. 31
Branchiocerianthus imperator (Allman, 1885); MHNG INVE 54660. (A) Blastostyle. (B) Tip of blastostyle with nematocyst cluster (arrow) and two incipient gonophores (g).

BIOLOGY: Recorded from depths of 200 to 4155 m.

DISTRIBUTION: North Pacific (Allman, 1888), Japan (Allman, 1888; Miyajima, 1900; Stechow, 1909a; Omori & Vervoort, 1986), off Somalia (Chun, 1900), Moçambique (Vervoort, 1966), North Atlantic SW of Ireland (Omori & Vervoort, 1986). Type localities: off Yokohama, Japan, 34.617°N 140.533°E, 3422 m depth and North Pacific, 37.683°N 177.067°W 5293 m depth.

REMARKS: See comments above under genus *Branchiocerianthus*. The species has been recorded only once in the Atlantic (Omori & Vervoort, 1986). The identification was made from photographs made by a submersible and relied basically on the size of the animal (>1 m).

Branchiocerianthus norvegicus Brattström, 1957 Fig. 32

Branchiocerianthus norvegicus Brattström, 1956: 1360. – Brattström, 1957: 3, pls 1-2. – Brattström, 1972: 99, figs 1-2.
? *Branchiocerianthus norvegicus*. – Vervoort, 1972: 13.

DIAGNOSIS: Atlantic *Branchiocerianthus* species measuring around 12 cm in height, outline of oral disk oval to circular, stem joining hydranth near its rim of the hydranth (very excentrical), about 54 aboral tentacles, blastostyles branched.

DESCRIPTION (Brattström, 1957; 1972): Hydrocaulus thin, widening basally and ending in a bulbous swelling bearing anchoring filaments. Stem with longitudinal gastrodermal canals, visible from outside as longitudinal striation.

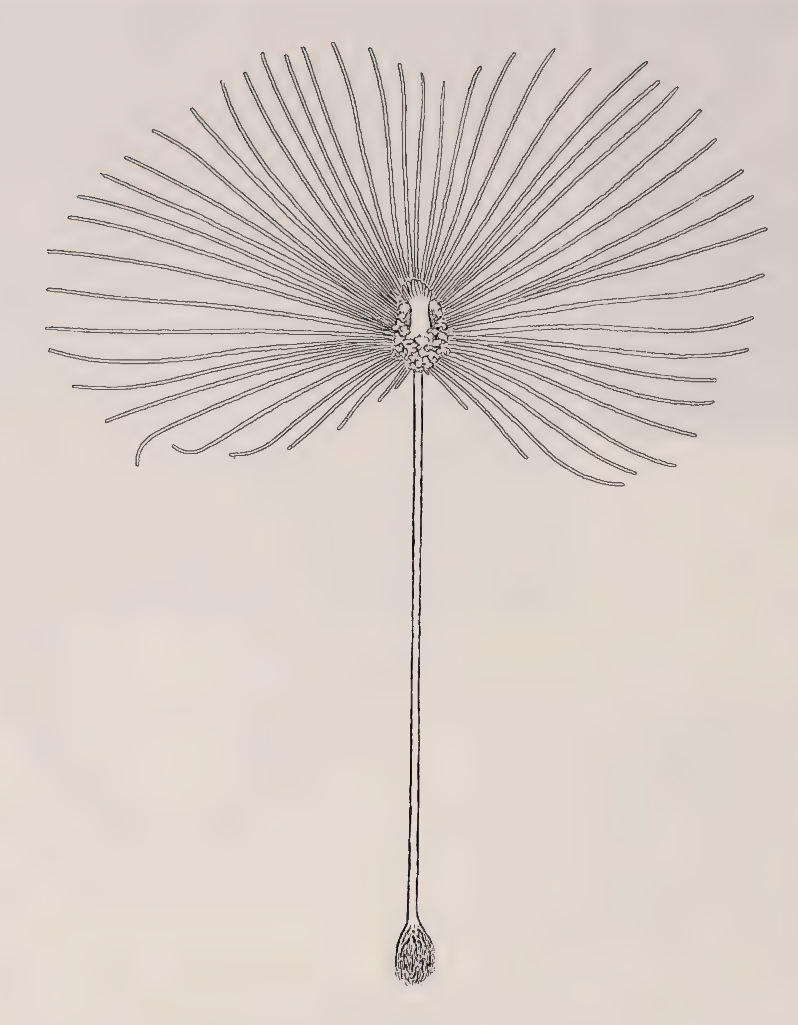


FIG. 32

Branchiocerianthus norvegicus Brattström, 1956; redrawn from Brattström (1957), height of polyp 10 cm.

Hydranth bilaterally symmetric, outline oval, longer axis in plane of symmetry, with an excentric ("ventral") insertion of hydrocaulus and an excentric ("dorsal") hypostome; hydranth attached obliquely to hydrocaulus. Hypostome at acute angle to oral disk. Aboral tentacles about 54 in number, in one whorl, the series broken in the ventral position where new tentacles develop. Oral tentacles short, 40-60 in number, in several whorls.

Blastostyles about 34 in number, in 1-2 rows above aboral tentacles, the youngest and shortest "ventral", branching dichotomously several times. Gonophore unknown as all known animals juvenile. Colours: pale pink, blastostyles pale salmon-red.

DIMENSIONS: Total height about 12 cm. Hydranth length 9 mm and breadth 7.5 mm to 12 x 12 mm. Maximal length of aboral tentacles 65 mm.

BIOLOGY: Depth range 210-3987 m (Vervoort, 1972).

DISTRIBUTION: Norway (Brattström, 1957; 1972), ? South Shetland Islands (Vervoort, 1972). Type locality: Norway, Hardanger Fjord, 60.4347°N 06.5639°E, 210-240 m, bottom of muddy sand and stones.

REMARKS: Brattström (1957) distinguished *B. norvegica* from *B. imperator* using the smaller size (12 cm versus 23-224 cm) and the more oval than round outline of the hydranth. The second specimen described by Brattström had a circular hydranth. The specimens of *B. norvegica* were clearly juvenile as no gonophores were yet present. The size difference to *B. imperator* might thus be due to the developmental stage.

Branchiocerianthus norvegicus and *B. italicus* as we know them today are not distinguishable and they are likely conspecific. For biogeographic reasons and because the two species might perhaps also differ in their so far unknown gonosome, it is preferable to retain the name for the time being. See also discussion under *B. italicus*.

Branchiocerianthus italicus Stechow, 1921b Figs 33-35

Branchiocerianthus. – Lo Bianco, 1909: 540.
Branchiocerianthus italicus Stechow, 1921b: 250. – Brinckmann-Voss, 1970: 22. – Bouillon *et al.*, 2004: 91.

MATERIAL EXAMINED: MHNG INVE 39464; Mediterranean, Algeria, Bay of Arzew, depth 320 m; collected 18.12.1955; about 10 not well preserved polyps.

DIAGNOSIS: Mediterranean *Branchiocerianthus* species measuring 10-15 cm in height, outline of oral disk oval, stem joining hydranth near its rim of the hydranth (very excentrical), about 60 aboral tentacles, radial canals unbranched, blastostyles branched, without terminal nematocyst clusters, mature gonophores unknown.

DESCRIPTION OF EXAMINED MATERIAL: Material not well preserved, entangled and distorted, about 10 polyps. Stems thin, inside with about 10 peripheral canals, stem joining hydranth near rim of the hydranth (very excentrical). Basal perisarc and attachment filaments absent, likely lost during collection process.

Hydranth joined obliquely to stem, outline at site of aboral tentacles distinctly oval, up to 70 aboral tentacles in one whorl, the series interrupted in the ventral position where new tentacles develop. Manubrium round, displaced from centre of oral disk away from stem attachment. One row of blastostyles arising above aboral tentacles and close to them, arranged in a U form. Blastostyles dichotomously branched, terminal branches short, end with grape-like clusters of small, sac-like appendages containing unidentified spherical bodies (Fig. 34B), representing perhaps decaying gonophores (due to mechanical or temperature damage). Mature gonophores unknown. Terminal nematocyst clusters as in *B. imperator* could not be found, but perhaps eroded, scattered nematocysts present in blastostyles.

Nematocysts: two size classes of stenoteles; desmonemes; spherical haplonemes with clearly visible shaft in several large coils; oval ? haplonemes.

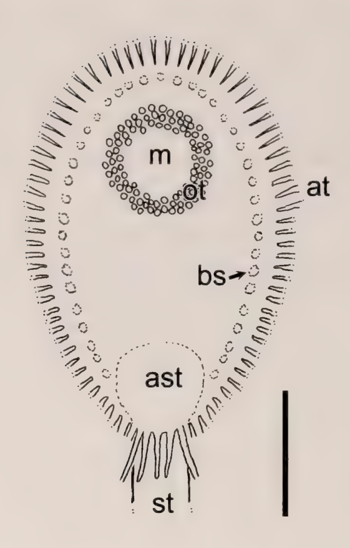


FIG. 33

Branchiocerianthus italicus Stechow, 1921b; hydranth organisation schema in oral view, drawn after preserved specimens (MHNG INVE 39464); scale bar 0.5 cm; *ast* attachment site of stem on underside, *at* aboral tentacles (cut), *bs* attachment sites of blastostyles, *ot* oral tentacles, *m* mouth, *st* stem (caulus).

DIMENSIONS: Largest specimens 10-12 cm, stem diameter about 2-3 mm, diameters of largest hydranths 14 x 8 mm, appendages on blastostyles up to 50 μm.

DISTRIBUTION: Mediterranean only. Type locality: Gulf of Naples, 300 m, on mud bottom.

REMARKS: Lo Bianco (1909) reported the finding of a *Branchiocerianthus* specimen from the Bay of Naples. He gave only a few details, like its size (10 cm) and colour (reddish). Most probably without having seen the material, Stechow (1921b) then introduced the name *B. italicus* for Lo Bianco's material. The species is thus rather indeterminate, or even of arguable validity. There are no subsequent records of *Branchiocerianthus* of the Mediterranean.

The available material for this study, coming from off Algeria, is unfortunately not well preserved. Like all other described *Branchiocerianthus*, the specimens had only incipient gonophore buds which did not allow any conclusion with regards to their mature morphology. With its pronounced oval hydranths and the size in the 10 cm range, the material is indistinguishable from *B. norvegicus* as described by Brattström (1957). The present material was attributed to *B. italicus* solely on the fact of its Mediterranean occurrence. Reproductive material from both Norway and the Mediterranean is needed for a further assessment of the status of both species. As long as the mature reproductive structures of all species are unknown, none of the nominal *Branchiocerianthus* species should be synonymized.



FIG. 34

Branchiocerianthus italicus Stechow, 1921b; preserved specimen (MHNG INVE 39464). (A) Blastostyle; scale bar 1 mm. (B) Terminal appendages of blastostyles filled with spherical bodies; scale bar 0.1 mm.

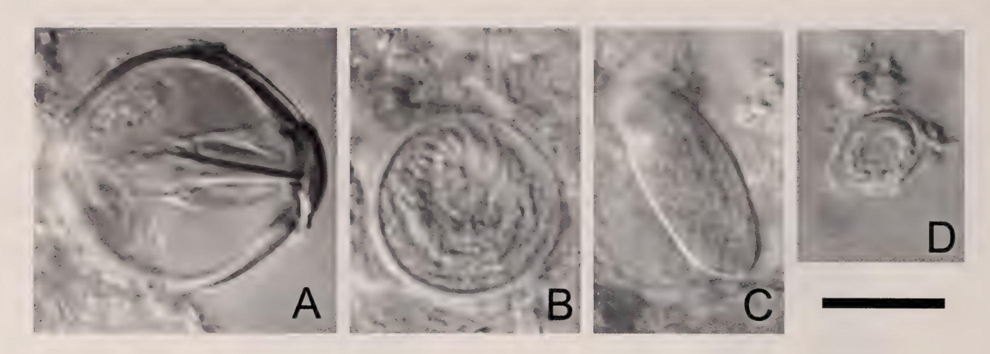


FIG. 35

Branchiocerianthus italicus Stechow, 1921b; nematocysts of preserved specimen (MHNG INVE 39464), scale bar 10 μm. (A) Large stenotele. (B) Spherical haploneme. (C) Oval ? haploneme. (D) Desmoneme.

Genus ***Euphysa*** Forbes, 1848

Euphysa Forbes, 1848; type species *Euphysa aurata* Forbes, 1848 by monotypy.
Heteractis Allman, 1864a; type species *Corymorpha annulicornis* M. Sars, 1860 by monotypy, preoccupied by *Heteractis* Milne Edwards & Haime, 1851 [Anthozoa].
Heterostephanus Allman, 1864b; type species *Corymorpha annulicornis* M. Sars, 1860 by monotypy.
Hypolytus Murbach, 1899; type species *Hypolytus peregrinus* Murbach, 1899 by monotypy.
Hypolitis Hargitt, 1901. [incorrect spelling]
Trichorhiza E. S. Russell, 1906; type species *Trichorhiza brunnea* E. S. Russell, 1906 by monotypy; preoccupied by *Trichorhiza* Hampson, 1905 [Insecta, Noctuidae].
Rhizotricha Stechow, 1919; type species *Trichorhiza brunnea* E. S. Russell, 1906; senior homonym of *Rhizotricha* Wolska, 1964 [Protista, Ciliophora].
Dahlgrenella Miles, 1937; type species *Dahlgrenella farcta* Miles, 1937 by monotypy.
Hipolytus Rees, 1946. [incorrect spelling]
Meiorhopalon Salvini-Plawen, 1987; type species *Meiorhopalon arenicolum* Salvin-Plawen, 1987 by monotypy.

DIAGNOSIS: Corymorphid hydroid with hydrocaulus enveloped in gelatinous perisarc, covered by mud and detritus; hydrocaulus hollow, without peripheral longitudinal canals. Hydranth cylindrical to ovoid, with rounded hypostome, with 3-10 oral capitate tentacles and up to 20 aboral moniliform tentacles, no gastric diaphragm. Near base of hydranth papillae, each with an ecto-endodermal, statocyst-like structure. Gonophores singly or in clusters just above aboral tentacles, usually released as free medusae, rarely remaining fixed as sporosacs.

Asexual reproduction through budding of polarity-reversed polyps from the hydranth above aboral tentacles and through asexual bodies constricted off from basal end of hydrocaulus.

Medusa with evenly rounded umbrella, without apical canal; with one to four tentacles, if more than one then usually unequally developed, but all of same structure, usually moniliform; manubrium stout, cylindrical with small round mouth, shorter than bell cavity.

REMARKS: The diagnosis of *Euphysa* follows largely Bouillon *et al.* (2006). Petersen (1990) included also *Euphysomma* Kramp, 1962 its synonymy. The systematic position of this genus cannot be evaluated adequately as long as its polyp stage

remains unknown. For discussion on of the genus see also Rees (1946), Kramp (1949) and Lindsay *et al.* (2008).

KEY TO THE *EUPHYSA* MEDUSAE OF THE ERMS ZONE

1a adult medusa with one moniliform tentacle only . . . . *E. aurata*
1b most adult individuals with more than one tentacle 2
2a three moniliform tentacles . . . . *E. tentaculata*
2b with four tentacles, all alike in adult but developing in succession . *E. flammea*

Euphysa aurata Forbes, 1848 Figs 36-37

Euphysa aurata Forbes, 1848: 71, pl. 13 fig. 3. – Kramp, 1926: 25, figs 21-22, pl. 1 figs 10-11. – Rees, 1938: 25, figs 8-9. – Russell, 1953: 90, figs 35E, 38-39, pl. 3 fig. 2. – Chow & Huang, 1958: 175, pl. 1 fig. 4. – Kramp, 1959: 85, fig. 29. – Kramp, 1961: 36. – Kramp, 1968: 10, fig. 14. – Russell, 1970: 233. – Brinckmann-Voss, 1970: 16, figs 12-15. – Schmidt, 1973a: 16. – Bouillon, 1974a: 143. – Pagès *et al.*, 1992: 20, fig. 19. – Schuchert, 2001a: 42, fig. 29. – Bouillon *et al.*, 2004: 101, fig 54A-D. – Galea, 2007: 29, fig. 7I, pl. 1K.
Corymorpha annulicornis M. Sars, 1860a: 96. – M. Sars, 1877: 8, pl. 1 figs 7-13. – Broch, 1937: 1-32, figs. 1-4, tab. – Rees, 1938: 25, synonym. – Westblad, 1947: 11.
Heterostephanus annulicornis. – Allman, 1872: 375.
Euphysa mediterranea Haeckel, 1879: 32, pl. 2 figs 8-9. – Hartlaub, 1907: 82, synonym. – Neppi & Stiasny, 1913: 8, synonym.
Trichorhiza brunnea E. S. Russell, 1906: 99, pl. 5. – Rees, 1938: 26, synonym. – Kramp, 1949: 192, synonym.
Corymorpha aurata. – Hartlaub, 1907: 81, figs 77-78. – Naumov, 1969: 228, figs 95-96.
Steenstrupia aurata. – Neppi & Stiasny, 1913: 8.
? *Dahlgrenella farcta* Miles, 1937: 327, plates 1-4. – Rees, 1938: 27, likely conspecific.
Heterostephanus spec. – Rees, 1937: 747, figs 1-3.
Heteractis aurata. – Kramp, 1949: 190, fig. 2.
Meiorhopalon arenicolum Salvini-Plawen, 1987: 623, figs 1-2. **new syn.**

TYPE MATERIAL EXAMINED: NHMW INVE #3038, 3 slides, labelled as typus of *Meirhopalon arenicolum*; Plymouth; preparation useless as no recognizable hydroid material present.

OTHER MATERIAL EXAMINED: Natural history museum of the Faroes; BIOFAR station 65; Faroes, 61.583°N 08.094°W, depth 322 m; 1 polyp collected 20.07.1987. – Scotland, Firth of Lorn, Dunstaffnage Bay, 56.455°N 05.434°W, surface plankton; several mature medusae collected 10-13 May 2004, examined alive, not preserved; 16S **FN687552**. – BMNH without number; Norway, Espegrend, depth 120 m; one polyp with medusa buds collected and identified W. J. Rees 09.08.1962. – BMNH 1985.3.8.2; two slides with label *Corymorpha nana* =? *Euphysa aurata*; Scotland, North Sea, Moray Firth, depth 45-60 m; 2 polyps with medusae bud; no collection date. – ZMUC without registration number; misidentified as *E. tentaculata*; Denmark, Frederikshavn; 7 medusae collected 31.07.1981. – BMNH 1939.12.2.84; slide labelled *Heterostephanus annulicornis*; Norway, Ypsø Sund, depth 70 m; one infertile polyp collected 09.08.1937, material described in Rees (1938). – MHNG INVE 48753; Norway, Fanafjord, close to southern coast, depth 60 m; 10 polyps with medusae buds; collected 16.06.2006, preserved as alcohol material and slide preparations; 16S **FN687553**. – Norway, middle of Fanafjord, surface plankton; one female medusa collected 22.06.2006, examined alive, used for DNA extraction; 16S sequence identical to **FN687553**.

DIAGNOSIS: Umbrella up to 4.5 mm high, higher than wide, jelly moderately thick, without gastric-peduncle, manubrium shorter than bell cavity, gonad covering almost whole length, females with few maturing ovocytes. With one moniliform tentacle only, three non-tentacular bulbs small.

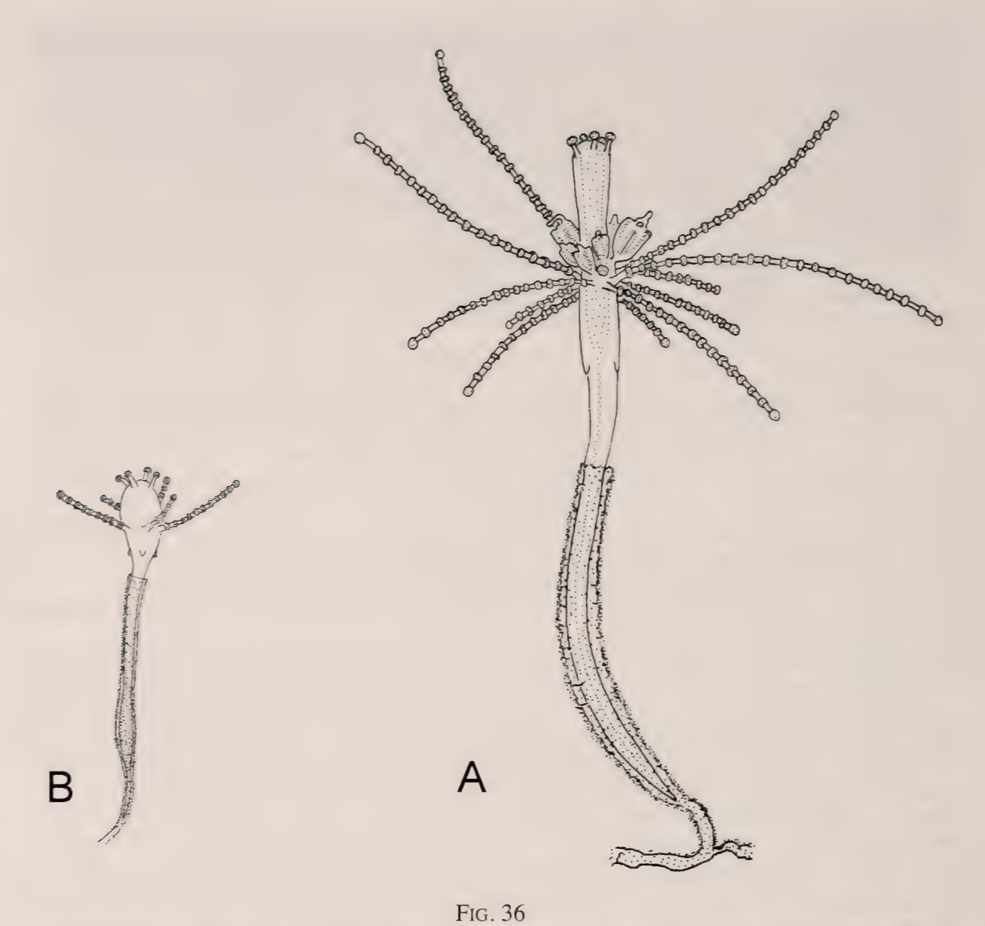


FIG. 36

Euphysa aurata Forbes, 1848; redrawn from Rees (1938). (A) Polyp with medusa buds, after live material, height approx. 4 mm. (B) Very young polyp derived from vegetative multiplication, size 1-2 mm.

DESCRIPTION: Polyps solitary, basal part usually embedded in sediment, very contractile (contracted only 1/5 of height). Composed of club-shaped hydranth and a tubular hydrocaulus, the limits of the hydranth and stem not always clearly marked. Stem tubular, tapering at base, covered by gelatinous membrane for the greater part, exterior always covered by adhering fine particles of mud; in lower part up to 10 scattered attachment filaments, may be absent; basal end may terminate in stolon-like processes allowing anchoring of the animal to objects and culture vessels. Basal part of stem can bud off fragments that grow into new, tiny polyps (asexual multiplication).

Hydranth tubular to ovoid, two whorls of tentacles, around mouth 3-8 oral tentacles, capitate, short and stubby, near middle of hydranth or slightly below 6-14 aboral tentacles in two closely approximated whorls, extensible, very long, sometimes as long as polyp height, shorter and longer ones alternating, all distinctly moniliform through numerous bead-like nematocyst clusters. Medusa buds develop in a broad band just above the aboral tentacles, buds directly attached to hydranth and no blasto-

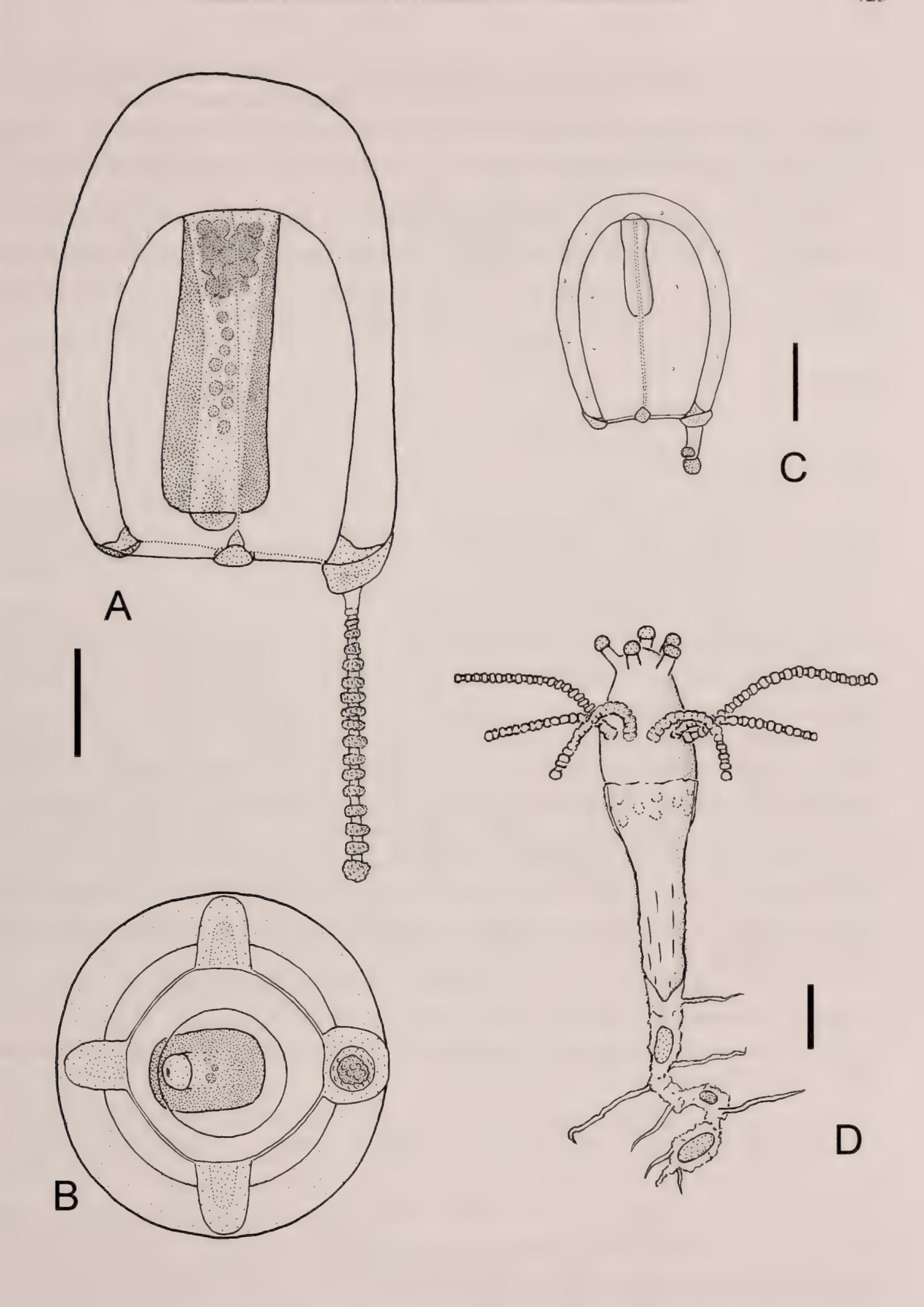


FIG. 37

Euphysa aurata Forbes, 1848. (A) Male medusa in lateral view, after living animal from Scotland, the spherical bodies in the stomach are oil droplets, scale bar 1 mm. (B) Same medusa in oral view. (C) Newly liberated medusa, drawn from life, scale bar 0.3 mm. (D) Polyp without medusa buds but with basal frustules, after preserved material from Greenland, scale bar 0.3 mm.

styles, buds not covered by envelope, advanced buds thus with their single tentacle standing out. At the aboral end of hydranth near junction to stem one or two whorls of 3-6 downward directed papillae, sometimes also a few similar papillae on stem, resembling rudimentary tentacles, some with a somewhat enlarged gastrodermal cell near the tip.

Hydranth may produce new polyps by budding small individuals in the medusa budding zone, the new polyps arise with a reversed polarity, their aboral side being directed away from the hydranth of origin. Asexual reproduction is also possible through bodies constricted off from basal end of hydrocaulus.

Nematocysts (Bouillon, 1985a): stenoteles, desmonemes, spherical anisorhizas, atrichous isorhiza, microbasic euryteles.

Colours: transparent light red.

Very young polyps with only four aboral tentacles, nematocyst clusters indistinctly moniliform, four short oral tentacles, four papillae near junction to stem.

Newly liberated medusa bell-shaped, some scattered nematocysts on exumbrella, manubrium short and cylindrical, without incipient gonads, four very thin radial canals, four marginal bulbs, one larger and bearing a short tentacles with a terminal swelling and 1-3 small, semicircular clasping nematocyst clusters.

Adult medusa umbrella bell-shaped, higher than broad, umbrella margin at right angles or slightly inclined towards vertical axis, apex rounded, without apical process, without apical canal; jelly relatively thick, especially in apical region; without exumbrellar nematocyst tracks; velum spans about half the radius. Manubrium cylindrical, 2/3 to nearly as long as subumbrellar cavity, mouth simple and surrounded by nematocysts, in upper half of manubrium numerous spherical oil-droplets; gonads surround manubrium completely, leaving only a small part free. Females with few large, amoeboid eggs. Four radial canals and ring canal rather thin. One single relatively short perradial tentacle, extended tentacle with 6-25 bead-like nematocyst clusters (= moniliform). Four marginal bulbs, three non-tentacular bulbs smaller than tentacular bulb, epidermal part flat, with nematocysts, extending as spur on exumbrella; gastrodermal chambers of bulbs rather shallow.

Colour of stomach, tentacle, and tentacular bulb a golden yellow, sometimes colourless or scarlet; subumbrella can be rose-coloured.

Nematocysts: stenoteles, desmonemes, microbasic euryteles, basitrichous isorhizas (Bouillon 1974).

Dimensions: Polyps in Atlantic when mature 1.2-4.5 mm high, hydranth 0.6-1.8 mm, diameter of hydrocaulus 0.2-0.5 mm (Rees, 1938; own data). Mediterranean polyps 1.3-1.5 mm (Brinckmann-Voss, 1970). Young asexually produced polyps up to 1.75 mm, but able to contract to much smaller sizes. Newly liberated medusa 0.6-1 mm high and wide. Most mature medusae of the Atlantic usually 3.5-4.5 mm high, width about 2/3 of height, known range of height is 2.5-6 mm. Egg size 0.4 mm (Norway). The Mediterranean medusae are smaller, 0.5-2.5 mm (Brinckmann-Voss, 1970; Goy, 1973).

Distribution: The medusa has been reported along the European coast from Brittany and the British Isles (absent in southeastern part of England), Norway (Hartlaub, 1907; Russell, 1953; Kramp, 1959), Kattegat (Kramp, 1926), Murmansk

coast (Kramp, 1926; Naumov, 1969), western Greenland (Kramp, 1959), and the Mediterranean (Neppi & Stiasny, 1913; Brinckmann-Voss, 1970; Palma, 1985). Outside this region, the medusa is also known from Massachusetts Bay, southern Africa, Patagonia, Chile, the Philippines, Malaysia, Mozambique, and the Red Sea (Kramp, 1968; Schmidt, 1973a; Bouillon, 1978a; Pagès *et al.*, 1992; Sparks & Gibbons, 2003; Buecher & Gibbons, 2003; Galea, 2007). The polyp stage has been documented from Brittany (Teissier, 1965), the British Isles (Rees, 1937; 1938; Russell, 1957), Norway (Rees, 1938; Christiansen, 1972; this study), the Arctic Sea (Naumov, 1969), western Greenland (Schuchert, 2001a), and the Mediterranean (Brinckmann-Voss, 1970). Type locality: Brassay Sound, Shetland Islands.

BIOLOGY: The polyp occurs in depths of a few metres to 630 m (usually deeper than 17 m), normally partially embedded in mud bottoms, rarely attached to holdfasts of seaweeds or red algae (Rees, 1938; Russell, 1957; Christiansen, 1972). The hydroid is present around Naples from November to April, quite abundant from December and February (Brinckmann-Voss, 1970). The medusa is not so common but can be found close to the shore and within the first metres of the water column. It is present from March to August in the British Isles, but may be found also later (Russell, 1953). Palma (1985) found evidence for diel vertical migrations of the medusa in the Bay of Villefranche. Some vertical migration was also observed for the population of southern Africa, but only for one of two observations periods (Buecher & Gibbons, 2003).

REMARKS: The taxonomic history and synonym of this species has been treated by Rees (1938) and Russell (1953). The species is nowadays well defined, but some problems remain. Forbes (1848) depicts the medusa with a short tentacle opposite the large tentacle, something that has never been reported for this species. It could have been a misinterpretation of the abaxial spurs of the marginal bulbs.

Meiorhopalon arenicolum Salvini-Plawen, 1987 appears indistinguishable from young polyps of *E. aurata* (e. g. Fig. 36B, or in Rees, 1938; Westblad, 1947; Brinckmann-Voss, 1970), except for the reversed polarity of the polyp bud. Figure 1 in Salvini-Plawen (1987) shows a polyp bud with its oral tentacles apparently facing away from the mother-hydranth, unlike in Rees (1937b) or Brinckmann-Voss (1970). The animals of Rees (1937b) and Salvini-Plawen (1987) came from both from the Plymouth Sound and I suspect that the polarity of the buds shown in Salvini-Plawen (1987) is perhaps an observation error. A re-examination of the type material was not helpful as the examined slides did not contain any material recognizable as parts of a hydroid. *Meiorhopalon arenicolum* is here interpreted as a juvenile *Euphysa aurata* polyp.

Euphysa tentaculata Linko, 1905 Figs 38-39

? *Euphysa virgulata* A. Agassiz, 1865: 189, figs 316-319.
? *Corymorpha pendula*. – A. Agassiz, 1865: 192, fig. 324. [not *Corymorpha pendula* L . Agassiz, 1862: 276, pl. 26 figs 7-17]
Euphysa tentaculata Linko, 1905: 214. – Kramp, 1926: 22, figs 17-20, pl. 1 fig. – Kramp, 1961: 38. – Arai & Brinckmann-Voss, 1980: 8, fig. 3.
Corymorpha tentaculata. – Naumov, 1969: 229, fig. 97. – Vervoort, 2009: 771.

MATERIAL EXAMINED: Norway, Raunefjord, 0-20 m depth, 19.06.2006; 1 male medusa, height 5 mm, 3 tentacles; not preserved, used for DNA extraction and nematocyst examination,

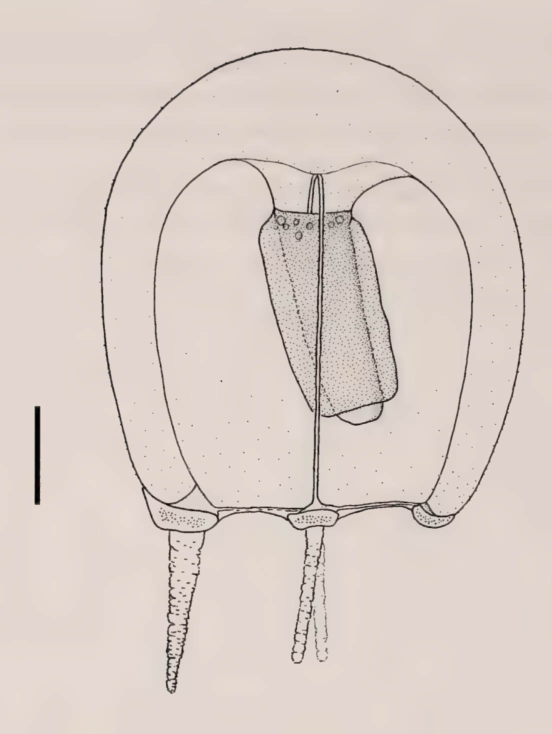


FIG. 38
Euphysa tentaculata Linko, 1905; lateral view of a fully grown male medusa, the spherical bodies in the manubrium are oil droplets, drawn after life, scale bar 1 mm.

16S sequence **FN687554**. – Norway, Fanafjord, 0-140 m, 22.06.2006, one subadult male, bell height 3.5 mm, one tentacle only; not preserved, used for DNA extraction, resulting 16S sequence identical to **FN687554**.

DIAGNOSIS: Umbrella up to 6 mm high, quite globular, jelly thick, with short gastric-peduncle in fully grown animals, manubrium shorter than bell cavity, gonad covering almost whole length, females with up to 25 ovocytes. With three tentacles, irregularly moniliform, one long tentacle and two short tentacles, one small bulb without tentacle.

DESCRIPTION: Medusa umbrella bell-shaped, rather globular, umbrella margin at right angles or slightly inclined towards vertical axis, apex rounded, without apical process or apical canal; jelly thick, especially in apical region, with short gastric peduncle in fully grown animals (length about 1/9 of height of subumbrellar cavity), peduncle absent in younger animals; without exumbrellar nematocyst tracks, velum spans about half the radius.

Manubrium cylindrical, about 3/5 as long as subumbrellar cavity, often held oblique to bell axis, mouth simple and surrounded by nematocysts, in upper half of manubrium numerous spherical oil-droplets; gonads surround manubrium completely,

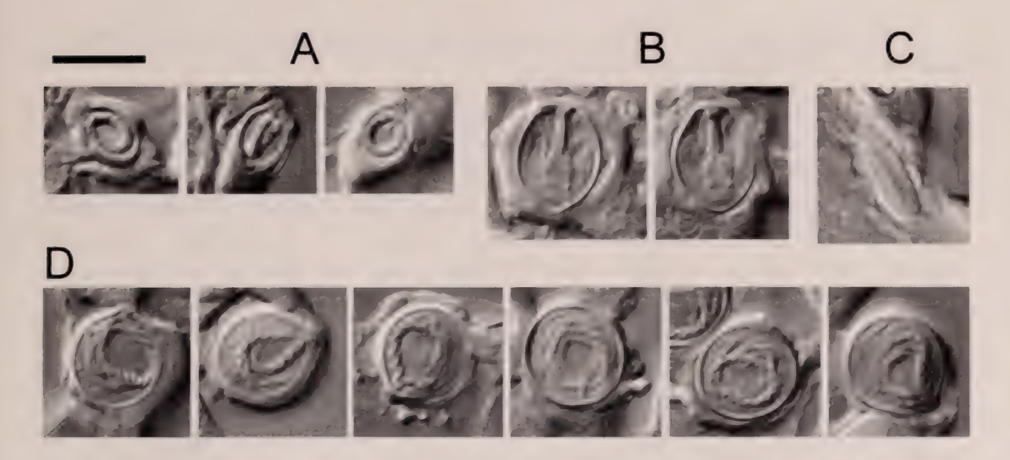


FIG. 39

Euphysa tentaculata Linko, 1905; dried and rehydrated tentacular nematocysts of the medusa shown in Fig. 38, scale bar 10 μm. (A) Desmonemes. (B) Stenoteles. (C) Microbasic heteroneme. (D) Anisorhizas.

leaving only a little part free. Females with up to 25 larger ovocytes. Four radial canals and ring canal rather thin.

Usually with three tentacles, irregularly moniliform, rarely and in very young animals only one tentacle. When three tentacles present, one tentacle longer and thicker than others, tapering when contracted, two shorter and thinner tentacles on bulbs closest to bulb with main tentacle.

Four marginal bulbs clasping umbrella margin, bulb with main tentacle almost two times larger than others, epidermal part of bulb with nematocysts, extending as short spur on exumbrella; gastrodermal chamber of main tentacle conical and well formed, others rather shallow.

Nematocysts: desmonemes; stenoteles; spherical heterotrichous or basitrichous anisorhizas, filament tapering rather distally; rare almond-shaped microbasic heteronemes (not seen discharged).

Atlantic medusae with yellow to orange bulbs and manubrium. Pacific medusae colourless or scarlet manubrium and tentacular bulbs (Arai & Brinckmann-Voss, 1980).

DIMENSIONS: Umbrella of adult medusa 4 to 6 mm high, slightly less wide, about 3.5-5.5 mm. Desmonemes (5.5-6.5)x(3.5-4.5)μm, stenoteles (11-13)x(8-9)μm, heteronemes (11)x(4)μm, anisorhizas (11-12)x(9.5-11)μm.

OTHER DATA: Kramp (1926) reports on some histological and microanatomical observations.

DISTRIBUTION: A rare circumpolar species penetrating into northern boreal regions, recorded from the Arctic Sea north of Russia, Greenland (Davis Street), Norway, Denmark (Kattegatt, Belt Sea), western Baltic; Pacific coast of Canada (Kramp, 1926, 1961; Naumov, 1969; Arai & Brinckmann-Voss, 1980). Type localities: Barents Sea, 68.90°N 42.583°E and 70.75°N 35.467°E (Linko, 1905).

BIOLOGY: In Danish waters the medusa can be encountered from May to July, but it is always rare (Kramp, 1926).

REMARKS: The polyp stage of *E. tentaculata* remains unknown (see also remarks under *C. nana*). Hartlaub (1907, 1917) and Mayer (1910) suggested that *Corymorpha pendula* Agassiz could be conspecific with *E. tentaculata*. The name *Corymorpha pendula* was introduced by L. Agassiz (1862) for a corymorphid hydroid with sporosacs which were not released and spawned on the hydroid. Alexander Agassiz (1865) then nevertheless used the same name for a medusa he found in the plankton and for which he clearly states that the link to the polyp of the same name is not proven. The medusa described in A. Agassiz (1865) as *C. pendula* could indeed be the same as *A. tentaculata*, however, it is certainly clearly distinct from *C. pendula* sensu L. Agassiz, 1862. L. Agassiz does not mention nematocyst band on the exumbrella, but Mayer (1910) mentions them in his description. He thus likely referred again to a different, third species.

Euphysa virgulata A. Agassiz, 1865, much resembles *E. tentaculata*, but has a bell size of 12 mm, which is twice the size of *E. tentaculata*. The identity of the two nominal species is thus questionable and a detailed examination of the *Euphysa virgulata* is needed in order to establish its relationships. I cannot agree with Mayer (1910) that *E. vigulata* is possibly referable to *E. aurata*, as A. Agassiz defined the genus as having three tentacles and he also depicts his medusa with three tentacles.

Kramp (1926) noted that younger specimens of *E. tentaculata* have only a single tentacle. I made the same observation for specimens collected near Bergen, Norway. The one-tentacled medusa of *E. tentaculata* formally resembles *E. aurata* and can thus be confounded with the latter species. In particular, preserved material might be difficult to separate. The one-tentacled specimen examined for this study was collected together with typical *E. aurata* medusae and the living medusae could be distinguished easily when compared side by side. *Euphysa tentaculata* has a distinctly more rounded umbrella and a thicker jelly (comp. Figs 37 and 38). In the compared animals, *E. tentaculata* had a darker yellow-orange colour and more exumbrellar nematocysts. The 16S DNA sequences obtained from the one- and the three-tentacled medusae were identical and clearly distinct from *E. aurata* (see Fig. 1).

Euphysa flammea (Hartlaub, 1902) Fig. 40

in part *Codonium princeps*. – Levinsen, 1893: 143.
in part *Sarsia brachygaster* Grönberg, 1898: 459, pl. 27 figs 3-4.
? (? *Syndiction*) *incertum* Linko, 1900: 139, pl. 1 fig. 1. – Mayer, 1910: 106, possible synonym.
Tiaridae. – Linko, 1902: 162, figs.
Sarsia flammea Hartlaub, 1902: 689. – Linko, 1905: 212. – Hartlaub, 1907: 12, figs 4-6. – Mayer, 1910: 64, fig. 27. – Bigelow, 1920: 4H, pl. 2 fig. 5. – Kramp & Damas, 1925: 244, figs 1-2.
Tiara spec. – Maas, 1904: 13, pl. 2 fig. 11.
Pandea maasi Mayer, 1910: 119, new name for *Tiara* spec. Maas, 1904.
Euphysa flammea. – Kramp, 1926: 19, pl. 1 figs 12-14. – Kramp, 1959: 85, fig. 31. – Kramp, 1961: 37. – Kramp, 1968: 10, fig. 16. – Arai & Brinckmann-Voss, 1980: 7. – Lindsay *et al.*, 2008: 1526, Fig 7.
in part *Sarsia japonica*. – Uchida, 1927: 181, fig. 24. [not *Euphysa japonica* (Maas, 1909)]
Sarsia japonica. – Kramp, 1928: 30, figs 2-7. – Uchida, 1933:127, fig. 3. [not *Euphysa japonica* (Maas, 1909)]

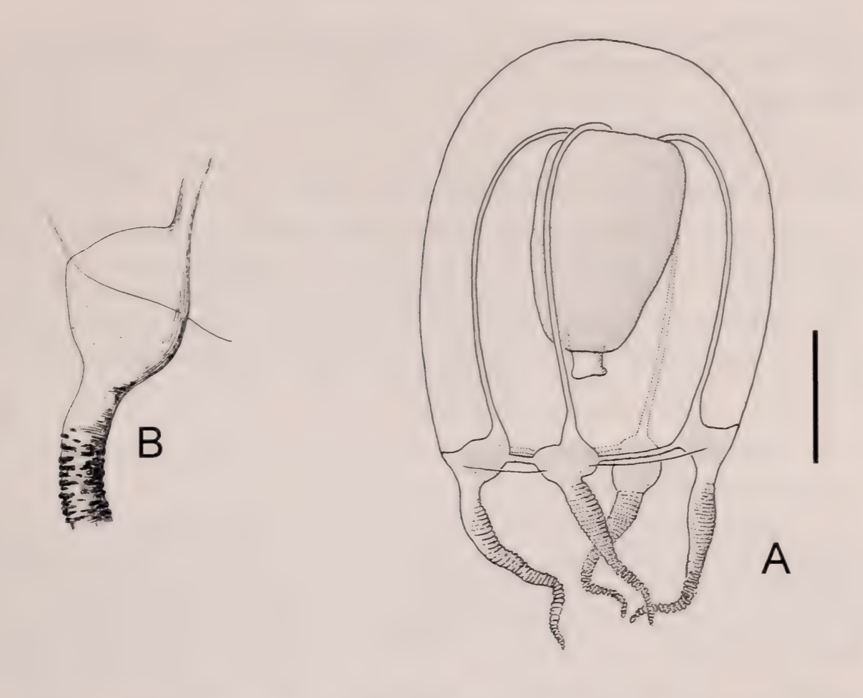


FIG. 40

Euphysa flammea (Hartlaub, 1902) (A) Mature medusa, redrawn from Naumov (1969), scale bar 5 mm. (B) Tentacle bulbs and proximal part of tentacle, from Hartlaub (1907).

in part *Sarsia flammea*. – Foerster, 1923: 221, pl. 1 fig. 1.
in part *Corymorpha flammea*. – Naumov 1969: 230, fig. 98, pl. 29 fig. 4.
not *Euphysa flammea*. – Goy *et al*., 1991: 104, fig. 10.
not *Euphysa flammea*. – Bouillon *et al*., 2004: 101, fig. 54A-D.

MATERIAL EXAMINED: ZMUC, without registration number; Greenland, 64.438 °N 50.233°W, 80 m depth; 1 medusa collected 15.06.1925. – ZMUC, without registration number; Greenland, north of Frederikshåb, collected 02.07.1909 with 100 m wire out; 10 badly preserved medusae. – ZMUC, without registration number; Norway, north of Vardø, 1 medusa collected 31.07.1907, leg Damas.

DIAGNOSIS: *Euphysa* medusa up to 15 mm high, umbrella bell-shaped, ratio of height to width less than 1.5, fully mature with four tentacles, all alike in adult, but developed in succession, youngest stages with only one tentacle, a second, third and fourth added successively; bulbs of equal size; manubrium intensely red, shorter than bell cavity.

DESCRIPTION (Linko, 1905; Kramp, 1926; Lindsay *et al*., 2008; own data): Fully grown medusa with evenly rounded umbrella, ratio of height and width 1.2-1.5 in healthy specimens, jelly thick, at top $^{1}/_{4}$ to $^{1}/_{3}$ of total height, without apical canal, some dispersed nematocysts on exumbrella, more in smaller animals.

Manubrium cylindrical, not extending beyond umbrella margin, near mouth often a slight constriction, mouth simple, circular, beset with nematocysts. Inside of

manubrium with four longitudinal processes. Gonads encircle manubrium along almost its entire length, leaving only part near mouth free, undivided, females with few large eggs.

Four marginal tentacles of similar length, in juveniles one long and three shorter tentacles, all of same irregularly moniliform structure, region of tentacles close to bulb narrowing, tentacles thus well demarcated from bulb.

Four distinct radial canals and ring canal, more or less smooth, four relatively large, equally developed, abaxially protruding marginal tentacle bulbs, without ocelli.

Colours: manubrium intensely red to orange, tentacle bulbs orange-red to yellow, tentacles pale orange, sometimes green, distal ends sometimes pale blue.

Younger stages (size 5-6.5 mm) may already have developed gonads, but still have one tentacle or unequally developed tentacles.

Polyp stage and cnidome unknown.

Dimensions: In the North Atlantic 6-15 mm high, 4-12 mm wide; in Alaska up to 19 mm high (Bigelow, 1920).

Distribution: Arctic circumpolar species penetrating into northern boreal regions, reaching southwards to Newfoundland in the western Atlantic, to northern Norway in the eastern Atlantic, to Vancouver Island in the eastern Pacific, and to northern Japan in the western Pacific (Linko, 1905; Hartlaub, 1907; Bigelow, 1920; Kramp & Damas, 1925; Kramp, 1926, 1961; Naumov, 1969; Zelickman, 1972; Lindsay *et al.*, 2008). Type locality: Barents Sea (Linko, 1905).

Biology: This is a common neritic species in the Arctic Ocean and most often found in catches between 0-200 m (Naumov, 1969). Rutherford & Thuesen (2005) studied the metabolic rate.

Remarks: Linko (1905) is usually credited as author of the name, certainly following the influential synopses of Kramp (1959, 1961, 1968). However, it was actually Hartlaub who introduced the name. Linko (1902) summarily described a medusa but did not name it, he just allocated it to the Family Tiaridae. Hartlaub (1902) reviewed Linko's paper in a subsequent short note and said that he has seen the same species before and that he will name it *Sarsia flammea* in a forthcoming publication. The name *Sarsia flammea* is clearly stated and referring to Linko's material. The introduction of the name *S. flammea* should thus be credited to Hartlaub, but the type material consists of Linko's (1902) specimens. Linko (1905) subsequently published a more detailed description using the name given by Hartlaub and also accepting Hartlaub's priority. The manuscript of Hartlaub mentioned in his note of 1902 was published later in 1907.

A first account of the taxonomic history and a review of the species were provided by Kramp (1926). He showed that this species does not belong to the Corynidae but the Corymorphidae. Kramp (1926) re-examined one specimen of the type series of *Sarsia brachygaster* Grönberg, 1898 and found that it belongs to *E. flammea*. Grönberg's description matches actually rather well *E. flammea*, except for the fact that he saw very small ocelli on the tentacle bulbs. The large size of his animals (15-19 mm), an exceptional size for most Corynidae, suggests that all his specimens could have been *E. flammea* and he might have misinterpreted some pigment in the bulbs as ocelli.

Linko (1902, 1905) described the gonad of *E. flammea* as perradially subdivided. The division of the gonad into four interradial parts is only apparent as it is feigned by four longitudinal ridges formed by the gastrodermis. There is a slight sexual dimorphism as in the females these ridges are narrower. The gonad itself forms a continuous ring (Kramp & Damas, 1925).

Adult *Euphysa japonica* (Maas, 1909) and *E. flammea* have been considered indistinguishable (Kramp, 1928; Arai & Brinckmann-Voss, 1980). They reportedly differ in their juvenile stages, *E. japonica* having four tentacles from the very beginning on, while *E. flammea* starts with one tentacle only and the others developing only later (Kramp & Damas, 1926). Lindsay *et al.* (2008) recently revised *E. flammea* and *E. japonica* and they argue that even adult medusae can be distinguished based on the bell shape. *Euphysa flammea* has a wide bell, the ratio of height to width not exceeding 1.5, while *E. japonica* has a high, tubular bell with a height to width ratio over 2. Another character separating the two species is the transition zone of the bulbs into the tentacles. In *E. japonica*, the bulbs taper gradually into the tentacles, while in *E. flammea* the diameter decreases abruptly, often giving the impression of a slight constriction between tentacle and bulb. Lindsay *et al.* (2008) think that both species have been regularly confounded and some records of adult *E. japonica* were actually *E. flammea*. The synonymy given above reflects this view. Lindsay *et al.* (2008) also present some evidence that there could be more, undescribed species resembling *E. flammea* and *E. japonica*.

Euphysa flammea is an Arctic species which does not penetrate into boreal regions of the eastern Atlantic. Its southern limit is the northern tip of Norway. Goy *et al.* (1991) nevertheless reported *E. flammea* from the coast of Lebanon. Their medusae were only 1.5 mm high and had four equally developed tentacles. At this size, *E. flammea* should have one tentacle only. The Mediterranean record of *E. flammea* is thus almost certainly incorrect and refers to another species.

Genus ***Siphonohydra*** Salvini-Plawen, 1966

Siphonohydra Salvini-Plawen, 1966; type species *Siphonohydra adriatica* Salvini-Plawen, 1966 by monotypy.

DIAGNOSIS: Polyps living in interstitial spaces between sand grains, small, club-shaped, four short tentacles around distal mouth, without distinct capitation, alternating with an aboral whorl of four longer tentacles with parenchymatic gastrodermis, aboral tentacles indistinctly moniliform to filiform, gastrodermis parenchymatic. Polyp budding above aboral tentacles. Below aboral tentacles four papillae with gastrodermal core, covered by epidermal lappet. Gonophores unknown.

REMARKS: The genus is currently monotypic and its status is problematic; it could belong to *Euphysa*. See also below under remarks for *S. adriatica*.

Siphonohydra adriatica Salvini-Plawen, 1966 Fig. 41

Siphonohydra adriatica Salvini-Plawen, 1966: 166, figs. 2-3, 8-9. – Salvini-Plawen, 1987: 625, fig. 3. – Bouillon *et al.*, 2004: 102, fig. 54F.

TYPE MATERIAL EXAMINED: NHMW 3336, 2 slides labelled as type-specimen of *Siphonohydra adriatica*; Rovigno; one slide useless as no recognizable hydroid material present, other slide with serial thin sections of bad quality.

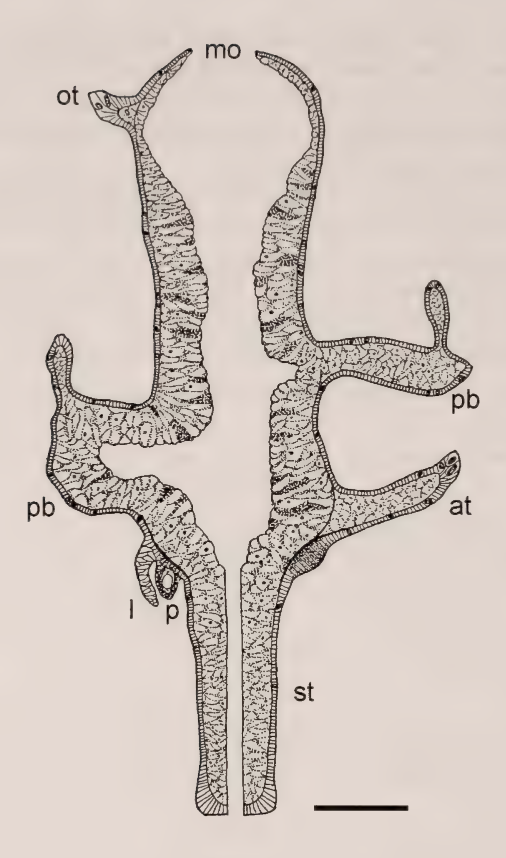


FIG. 41

Siphonohydra adriatica Salvini-Plawen, 1966; schematic horizontal section in plane of aboral tentacle (right) and between aboral tentacles (left); scale bar 0.1 mm; from Salvini-Plawen (1966). Abbreviations: *at* aboral tentacle, *l* lappet, mo mouth, *ot* oral tentacle, *p* protrusion with gastrodermal core, *pb* polyp bud.

DIAGNOSIS: See genus diagnosis.

DIMENSIONS: Total height of polyp 0.75-1.2 mm, caulus about 1/3 of the total height.

BIOLOGY: Found once in 6 m depth in coarse sand.

DISTRIBUTION: Known only from the type locality near Rovigno (Croatia).

REMARKS: Salvini-Plawen (1966) interpreted the bud-like appendages near the hydranth base of *Siphonohydra adriatica* as gonophores (Fig. 41, p), although neither gametes nor their precursors were present. Later (Salvini-Plawen, 1987), he identified these processes as "proximal bulges", likely representing static organs. Again, he did not observe statoliths and based his conclusion only on some resemblance to similar structures in *Euphysa ruthae* (Norenburg & Morse, 1983). For both species there is no convincing structural and experimental evidence that these processes are indeed functional statocysts. The gonophores of *Siphonohydra* as well as the fully grown animal

thus remain unknown. A re-examination of the type material did not reveal any further details than not already given in the genus diagnosis (see also Fig. 41). The animal resembles young *Euphysa aurata* polyps and *Siphonohydra* may well be considered as congeneric with *Euphysa*. However, the gonophores of this animal must be known to assess the validity of the genus and species.

Genus ***Paragotoea*** Kramp, 1942

Paragotoea Kramp, 1942; type species *Paragotoea bathybia* Kramp, 1942 by monotypy.

DIAGNOSIS: Medusa umbrella with scattered nematocysts, single tentacle terminating in a globular nematocyst knob, four very large and prominent marginal bulbs with abaxial spurs, cylindrical or globular manubrium with simple circular mouth. Cnidome composed of stenoteles only.

REMARKS: This is a monotypic genus.

Paragotoea bathybia Kramp, 1942 Fig. 42

Paragotoea bathybia Kramp, 1942: 26, fig. 7a-c. – Kramp, 1959: 5, 91, fig. 43. – Kramp, 1961: 44. – Petersen, 1990: 134, fig. 8A-C. – Pagès & Bouillon, 1997: 487, figs 1-2, revision. – Brinckmann-Voss & Arai, 1998: 53, fig. 7. – Bouillon *et al.*, 2004: 93, fig. 49J.

not *Paragotoea bathybia*. – Ralph, 1959: 171, figs A-D.[= *Tetraralphia hypothetica* Pagès & Bouillon, 1997]

? *Paragotoea bathybia*. – Brinckmann-Voss, 1970: 21, figs 20-21. – Goy, 1973: 972, fig. 3.

Paragotoea elegans Margulis, 1989: 127, fig. 2A-E. – Pagès & Bouillon, 1997: 490, synonym of *P. bathybia*.

MATERIAL EXAMINED: MNHN no. 1620; France, Mediterranean, Villefranche-sur-Mer, 3 medusae collected 1963; material described by Goy (1973). Very small medusae, not suitable for a redescription.

DIAGNOSIS: *Corymorpha*-like medusa with a single stiff tentacle ending in spherical nematocyst knob, without gastric pouches, marginal bulbs very large and with abaxial spurs extending to a variable degree on exumbrella, no meridional nematocyst tracks on exumbrella.

DESCRIPTION (Pagès & Bouillon, 1997): Umbrella square or rectangular with a slightly conical apex containing refractile droplets, exumbrella with scattered nematocysts, no meridional nematocyst tracks on exumbrella, lateral exumbrellar walls and mesogloea of uniform thickness.

Manubrium broadly flask-shaped, sometimes globular, extending from half of the subumbrellar cavity to the umbrella margin depending on umbrella contraction, top part with large, vacuolated gastrodermal cells, mouth simple, circular, rim with nematocysts.

Gonads developing interradially in the lower half of the manubrium and in more advanced stages encircling manubrium entirely.

One stiff, tapering marginal tentacle with a basal thickening, proximal part hollow, distal part solid with very thick mesoglea, one terminal and globular knob of nematocysts.

Four conspicuous radial canals, enlarged distally with large gastrodermal cells, lumen very narrow, circular canal present. Four very large and prominent marginal

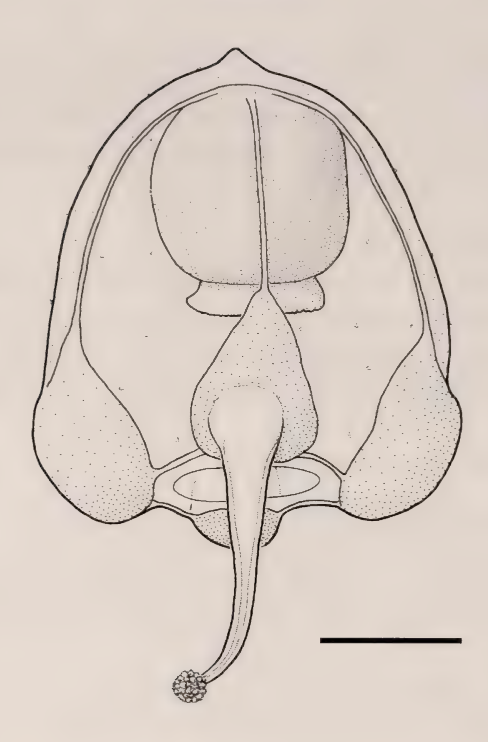


Fig. 42

Paragotoea bathybia Kramp, 1942; mature medusa from Antarctica, scale bar 0.5 mm, redrawn and modified from Pages & Bouillon (1997).

bulbs, one tentacular and three non-tentacular, all similar, tentacular bulb sometimes larger, all bulbs with abaxial spurs extending onto exumbrella, length of spurs variable.

Cnidome: stenoteles of two sizes.

Colour: transparent when alive, with green-yellow vacuolated cells in the inner part of the marginal bulbs.

Polyp stage unknown.

Dimensions (Pagès & Bouillon, 1997): Umbrella 0.5-2.0 mm high and 0.4-1.6 mm wide. Stenoteles 17.5 μm and 8.0 μm long.

Biology (Pagès & Bouillon, 1997): The medusa has been found in depths from zero to 2000 m, although the specimens collected in the Southern Ocean had a vertical distribution mainly between 700 and 200 m.

Distribution: Western Greenland (Kramp 1942); Arctic Sea (Margulis, 1989); Mediterranean (Brinckmann-Voss, 1970; Goy, 1973); South Africa (Kramp, 1959); Southern Ocean and Antarctica (Margulis, 1989; Pagès & Bouillon, 1997); British Columbia (Brinckmann-Voss & Arai, 1998). Type locality: Baffin Bay, western Greenland.

Remarks: Pagès & Bouillon (1997) revised and re-described *Paragotoea bathybia* based on several living medusae. They also made it clear that the fully grown

medusa has a single tentacle only, this in contradistinction to the interpretation of Ralph (1959). The four-tentacled medusa described in Ralph (1959) is a distinct species, namely *Tetraralphia hypothetica* Pagès & Bouillon, 1997, a view also approved by Brinckmann-Voss & Arai (1998).

Brinckmann-Voss & Arai (1998) further think that the Mediterranean records of *P. bathybia* belong to a separate, unnamed species. The specimens of Brinckmann-Voss (1970) had partially divided gonads and the terminal nematocyst cluster of the tentacle was divided into sector-like portions. According to Pagès & Bouillon (1997), the subdivision of the gonad could be due to the developmental stage. In younger stages they are divided, in older ones the parts get more and more fused. The Mediterranean sample examined for this study was unfortunately not suitable for a careful comparison, which should preferably be done with living material.

Family Paracorynidae Picard, 1957

Diagnosis: Hydroid with polymorphic hydranths, differentiated into gastrozooids, gonozooids, and dactylozooids. Polyps arising from crust-like basal plate, plate without perisarc, outer layer of epidermis envelopes thick gastrodermal layer with upper layer of broad gastrodermal cavities and basal layer of large, parenchymatic gastrodermal cells continuous with those in dactylozooids, transversed by mesogloeal lamellae. Gastrozooids short, stout, with one to four whorls of solid capitate tentacles; gonozooids short, lacking tentacles and mouth, bearing cryptomedusoid gonophores; eggs develop into actinulae within gonophore or into encysted resting stage; dactylozooids around edge of colony, long, finger-shaped, filled with parenchymatic gastrodermis.

Remarks: Bouillon (1974b, 1975) provides several good arguments that this family is related to the Tubulariidae. The family is monotypic.

Genus ***Paracoryne*** Picard, 1957

Paracoryne Picard, 1957; type species *Paracoryne huvei* Picard, 1957 by original designation.

Diagnosis: With the characteristics of the family.

Remarks: The genus is currently monotypic.

Paracoryne huvei Picard, 1957 — Figs 43-45

Paracoryne huvei Picard, 1957: 6. – Prévot, 1959: 105, pl. 4 fig. 14. – Brinckmann-Voss, 1970: 84. – Bouillon, 1974b: 9, figs 1-18, pls 1-3. – Bouillon, 1975: 45, figs 1-13, 17. – Boero, 1984: 106, figs 12-13. – Petersen, 1990: 202. – Bouillon *et al.*, 2004: 102, fig. 54 G.

Material examined: IRSNB IG 27.838; France, Var, east of île des Embiez, depth 0 m; fertile colonies collected April 1974; material of Bouillon (1975). – ZMUC, without registration number; France, Var, east of île des Embiez, Le Brusc; depth 0 m; fertile colonies on *Mytilus galloprovincialis* collected 06.06.1973, material identified and donated by J. Bouillon.

Diagnosis: See family diagnosis.

Description (Bouillon, 1974b, 1975; own data): Conspicuously coloured, large colonies living exclusively in the intertidal zone. Polyps arising densely from a common crust-like basal plate. Basal plate oval to round, without perisarc. Outermost layer the epidermal epithelium, inside an upper layer of flat, broad gastrodermal

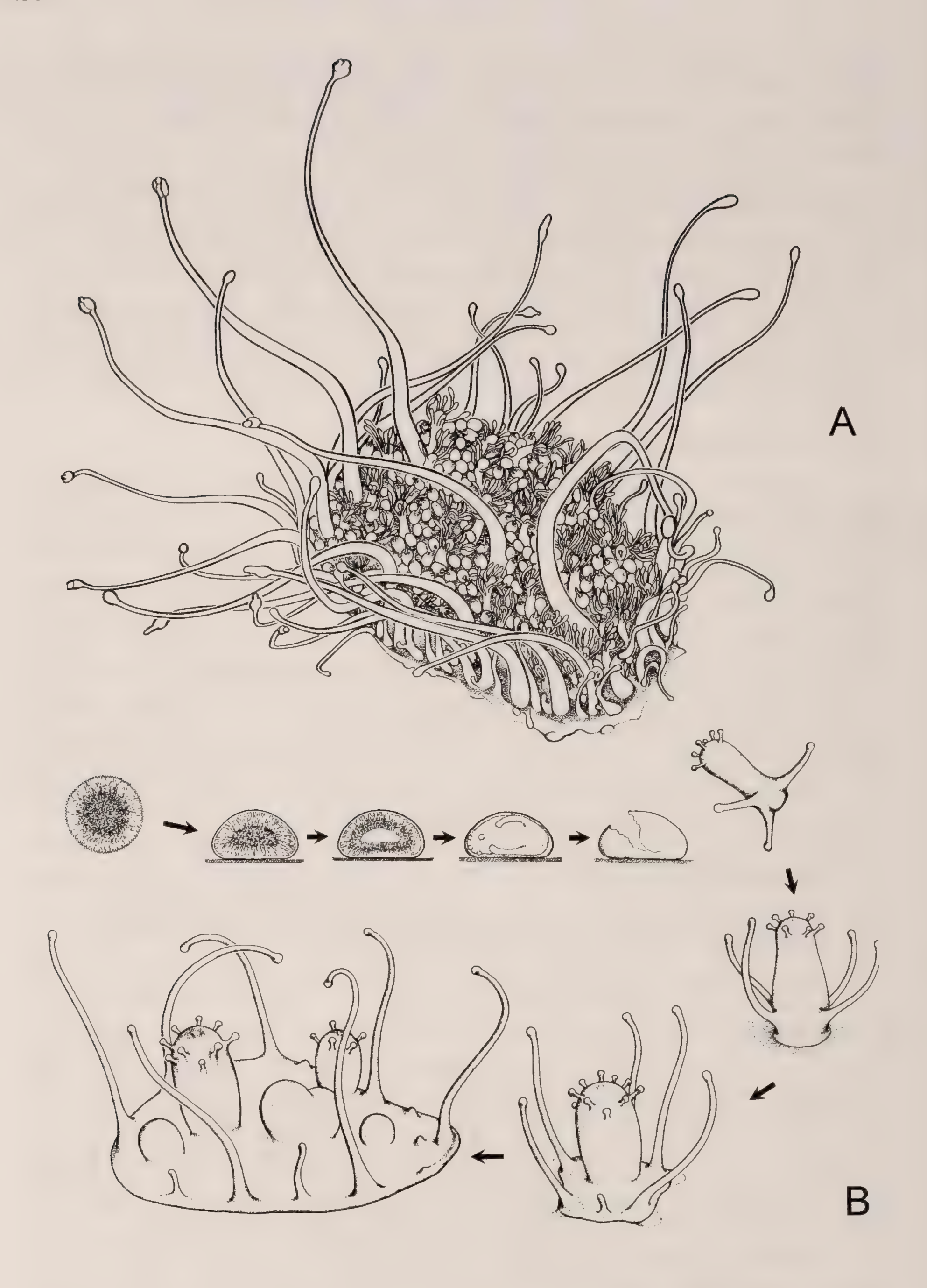


FIG. 43

Paracoryne huvei Picard, 1957; modified after Bouillon (1975). (A) Small reproductive colony. (B) Sexual cycle, clockwise, starting with stereogastrula, resting stages, developing actinula in capsule, hatched actinula, settled actinula, successive growth of initial colony.

cavities and canals which are continuous with the gastric cavities of the gastrozooids and gonozooids. Below layer of gastrodermal canals a thick layer of large, parenchymatic cells continuous with those inside the dactylozooids. Vertical mesogloeal lamellae transverse the layer of parenchymatic cells.

Polyps in a dense lawn on upper side of basal plate, distinctly polymorphic, differentiated into dactylozooids, gastrozooids, and gonozooids. Polyps all sessile and with wide base, thus without pedicel.

Dactylozooids more usually at periphery of colony but some also more in centre, large, up to ten times the size of gastrozooids, tentacle-like, tapering from basal to distal, terminal part often swollen, without mouth or gastric cavity, filled with large, parenchymatic cells. At basal region of dactylozooids internal whitish gastrodermal canals that form a ring with distal digitations.

Gastrozooids club-shaped or like bowling-pins, rounded hypostome, in distal third of polyp 1-4 irregular whorls of 14-23 tentacles, their length decreasing towards oral but lengths variable, oralmost tentacles short and stubby, slightly capitate, 2-7 in number, more proximal tentacles 8-20 in number, longer, usually filiform or distal end only slightly and gradually swollen. Gastrodermis in upper half of polyp with longitudinal folds projecting into lumen. Epidermis of oral zone and zone of tentacles with longitudinal lines of purple pigment issued from a ring around mouth.

Gonozooids small, short, reduced polyps, cylindrical, lacking mouth and usually also tentacles, occasionally one short indistinctly capitate tentacle present. At distal end of gonozoid 2-4 (females) or 2-10 (males) sporosacs, most advanced ones always distal, developing ones more proximal. Gonophores are cryptomedusoids (no radial canals, replaced by gastrodermal lamella), spherical to oblong, with short stalk, males when mature with a distal tubular process ending in the opening of the sporosac. Ring of purple pigment granules at distal end of sporosac, in fully mature ones encircling base of distal process. Female sporosacs also cryptomedusoids, initially with numerous oogonia, of which only 2-4 will develop into ovocytes. Fertilized eggs produce a periderm capsule (embryotheca), a resting stage in which the development to the actinula takes place. In the early reproductive phase, embryos may also develop into actinulas without encapsulation.

Nematocysts: stenoteles of different sizes; desmonemes; large euryteles with discharged shaft about 2.5-3 times as long as capsule thus approaching macrobasic condition; smaller microbasic haplonemes (mastigophores; shaft shorter than capsule, not swollen); atrichous isorhizas.

Colours: gastrozooids purple or dark brown.

Actinula stage after hatching from embryotheca with cylindrical body, functional mouth encircled by 3-7 short capitate tentacles, near aboral end one whorl of 3-5 long, slightly capitate tentacles. Actinula settles with aboral end and starts to produce the hydrorhizal plate (Fig. 43B).

Dimensions: Colony size up to 4 x 2 cm, basal plate about 1 mm thick, dactylozooids up to 15 mm high, gastrozooids 1.5-2 mm, gonozooids <1 mm, actinula 0.5 mm. For nematocyst dimensions see Bouillon (1974b).

Other data: Bouillon (1974b, 1975) provides a detailed account on many aspects of the biology of this species, including the morphology, histology, development, and ecology.

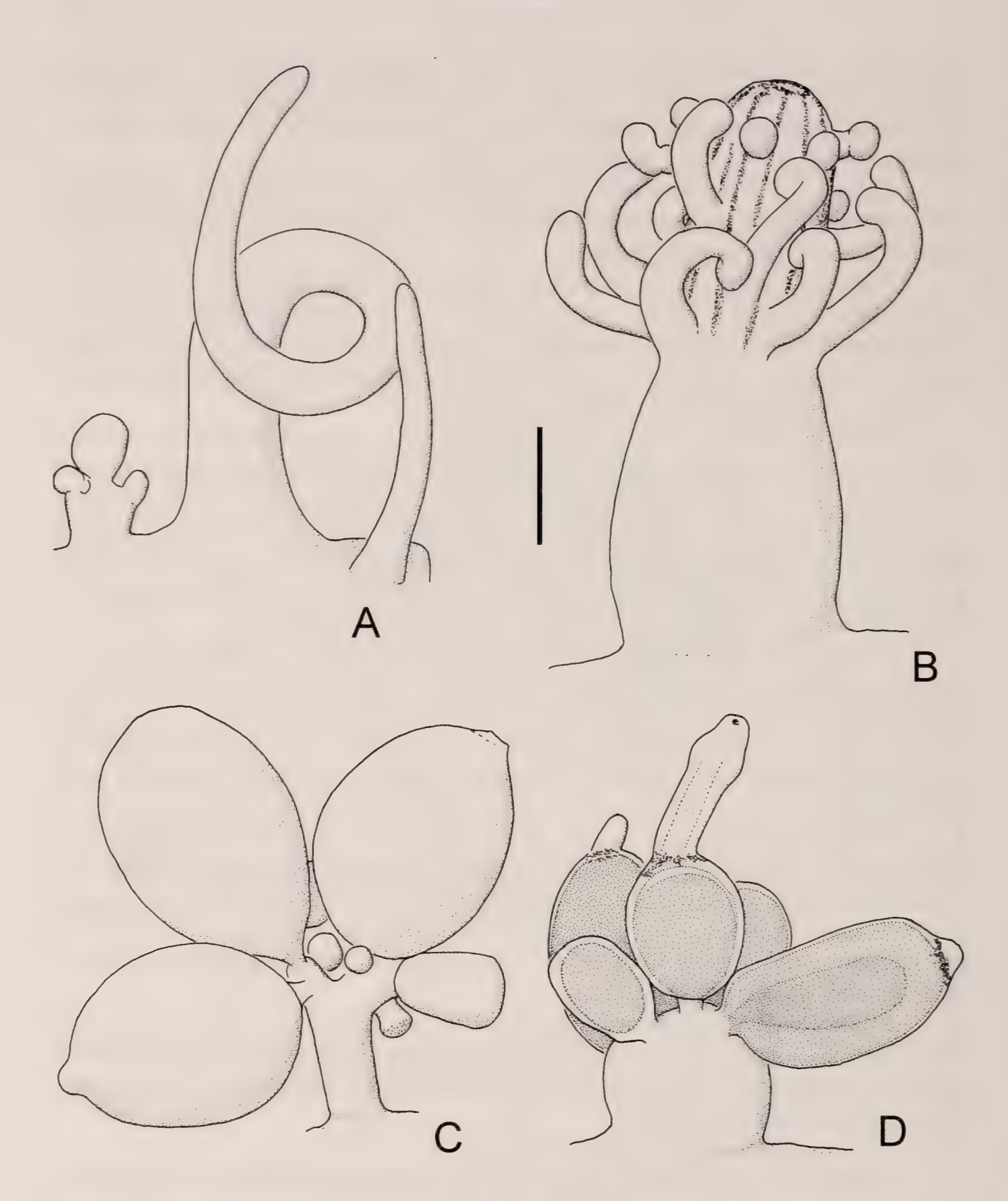


FIG. 44

Paracoryne huvei Picard, 1957; after preserved material. (A) Dactylozooids and one gonozooid at margin of colony, scale more than two times smaller than polyps shown in B-C. (B) Gastrozooid, scale bar 0.2 mm. (C) Gonozooid with female sporosacs, same scale as B. (D) Gonozooid with male sporosacs, sporosac with long process has partially spent its gametes, same scale as B.

BIOLOGY: This species occurs only sporadically, likely remaining dormant for years as resting stages. When present, it can occur in large numbers. Rather exceptional for hydroids, it lives within the tidal range, usually on rocks overgrown with coralline

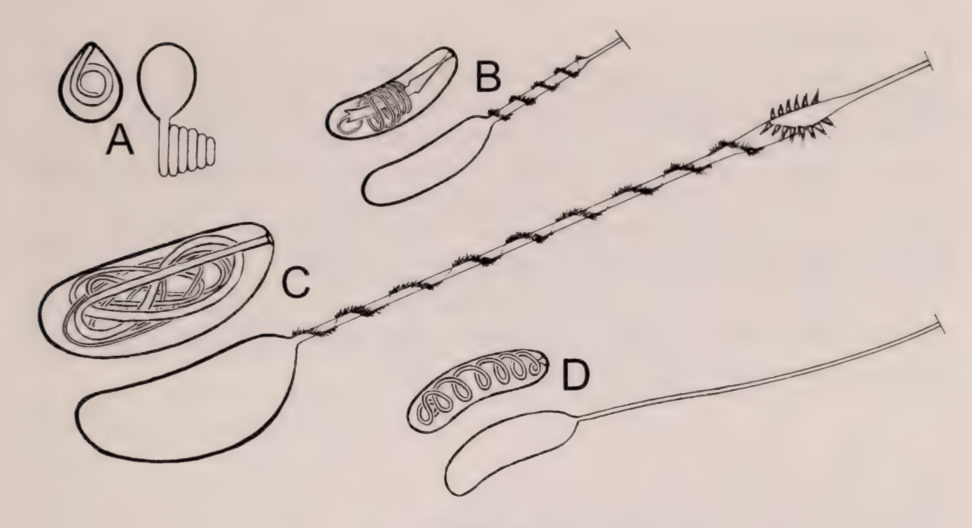


FIG. 45

Paracoryne huvei Picard, 1957; nematocysts as pairs of undischarged and discharged capsule, stenoteles not shown; after Bouillon (1974b). (A) Desmonemes, length about 4.5 μm. (B) Microbasic heteroneme, size about 9 μm. (C) Larger heteroneme (eurytele with long shaft), size about 14 μm. (D) Atrichous isorhizas, size about 9 μm.

algae, less frequently on *Mytilus* and barnacles. See Bouillon (1975) for more ecological data.

DISTRIBUTION: Western Mediterranean (Picard, 1957; Bouillon, 1974b, 1975; Boero, 1981; Medel & López-González, 1996). Type locality: Ligurian Sea, near Hyères, Ilot du Grand Ribaud and Cap Taillat.

REMARKS: A conspicuous, but rarely reported species. As it is easily seen and occurs in the intertidal zone, it seems unlikely that this species would have gone unnoted by earlier authors. One must thus assume that *Paracoryne huvei* occurs only sporadically and passes most of its time as resting stages.

The larger heteronemes (Fig. 45C) were identified by Picard (1957) as macrobasic euryteles, while Bouillon (1974b) used a somewhat different definition and qualified it as microbasic. This capsule is a good example of the fact that sometimes the nematocysts are not classifiable (for overviews see e. g. Russell, 1953; Werner, 1965; Millard, 1975; Schuchert, 1996; Bouillon *et al.*, 2006). The currently prevalent view is that macrobasic heteronemes have shaft lengths larger than 2.5 to 3 times the capsule length. The larger heteronemes fall exactly into this range and the capsule is thus not unambiguously nameable. Nematocyst morphologies are intergrading and they are not always classifiable like species. This is also evident for the smaller heteroneme of *P. huvei* which was identified as a eurytele by Bouillon (1974b), but figured as a mastigophore (Fig. 45B). Again, the mastigophore- and eurytele-type capsules are only extremes of a continuum and in many cases no unambiguous decision can be made on how to classify a capsule (Russell, 1953). In such cases it is better to use the more inclusive term heteroneme.

Family Hydridae Dana, 1846

Diagnosis: Solitary freshwater hydroids, tubular body, with hollow filiform tentacles, but often moniliform distally, in one whorl under hypostome; base of hydranth a small, flat pedal disc used for the attachment to the substrate, polyps lacking perisarc, perisarc formed only as capsule enveloping fertilized eggs and developing embryos. Without medusa phase or gonophore development, eggs and sperm developed directly in epidermis of polyps in wart-like protuberances, no planula stage; asexual reproduction by lateral buds, leading only to temporary colonies.

Remarks: In current taxonomic practice the family comprises only the genus *Hydra* (Holstein, 1995; Bouillon *et al.*, 2006). Holstein (1995) gives an excellent and comprehensive review of the European *Hydra* species.

Genus ***Hydra*** Linnaeus, 1758

Hydra Linnaeus, 1758; no type species designated.
Chlorohydra Schulze, 1914; no type species designated.
Pelmatohydra Schulze, 1914; no type species designated.

Diagnosis: As for family.

Remarks: The taxonomy of the European *Hydra* species has been studied by many authors and does not need to be repeated in detail here (e. g. Brauer, 1909; Schulze, 1917; Ewer, 1948; Grayson, 1971, Heitkamp, 1986; Campbell, 1989; Holstein, 1995; Campbell, 1999). The synonymy as given in Holstein (1995) is adopted here. Many biological details are also given in this monograph and they are not all repeated here. There are currently five valid European *Hydra* species (Holstein, 1995). A preliminary molecular phylogeny is given in Hemmrich *et al.* (2006).

A reliable identification of *Hydra* species requires an examination of the intact nematocysts. Of particular importance is the holotrichous isorhiza capsule (Figs 47F, 49F, 52F, 54F, 56F). Observation of these nematocysts requires a compound microscope with 1000-fold magnification (oil immersion).

Key to the European *Hydra* species:

1a polyps intensively green through symbiotic algae .... *H. viridissima*
1b polyps not green 2
2a holotrichous isorhiza ovoid, height/width ratio < 2 (Figs 49F, 50D) .... *H. circumcincta*
2b holotrichous isorhiza elongate-oval height/width ratio > 2 (Fig 52F) 3
3a shaft in holotrichous isorhiza coiled along long axis of capsule (Figs 52F, 53D), polyp with foot-region .... *H. oligactis*
3b first 3-6 coils of shaft in holotrichous isorhiza transverse or oblique (Figs 54F, 55D, 56F) 4
4a stenoteles rounded (Figs 54C, 55A) .... *H. vulgaris*
4b stenoteles markedly ovoid, upper part rather pointed (Figs 56C, 57) ... . *H. oxycnida*

Hydra viridissima Pallas, 1766 Figs 46-48

Hydra viridis Linnaeus, 1746: 367.
Hydra viridissima Pallas, 1766: 31. – Grayson, 1971: 441. – Heitkamp, 1986: 531, fig. 2. – Brien & Reniers-Decoen, 1951: 33, figs 1-25. – McAuley, 1984: 5, figs 1-2. – Holstein, 1995: 68, figs 8q-t, 21-24. – Campbell, 1999: 96, figs 1-2.
Hydra viridis Linnaeus, 1767: 1320.
Chlorohydra viridissima. – Schulze, 1914: 396, fig'd. – Ball, 1967: 82, figs 1-3.

Material examined: MHNG INVE 55116; Switzerland, small pond west of Geneva, 46.221133°N 06.28043°E, depth 0-0.2m; collected 15.09.2007; numerous infertile specimens, some preserved, some used for DNA extraction. – Same locality as before; collected 03.11.2003; infertile, not preserved, used for DNA extraction. – Same locality as before; collected 14.06.2008; several fertile hermaphrodites; not preserved. – Same locality as before; collected 31.01.2010, pond partially frozen; 2 infertile specimen; not preserved.

Diagnosis: Small *Hydra*, green due to zoochlorellae, holotrichous isorhizas elongated, ratio length-width about 2, thread forming 3-4 ordered coils in upper part of capsule.

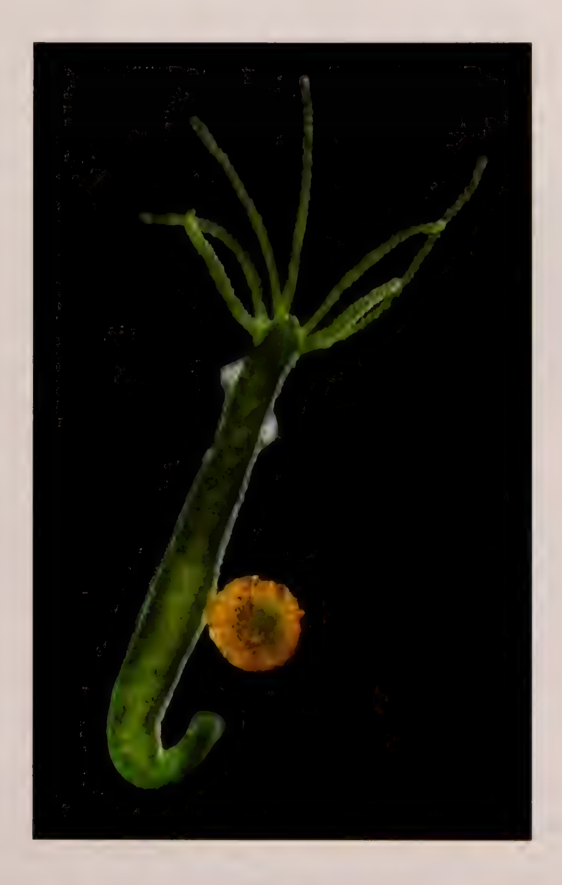


Fig. 46

Hydra viridissima Pallas, 1766; living animal, about 3 mm, with male gonads (white) and an encapsulated embryo (brown sphere).

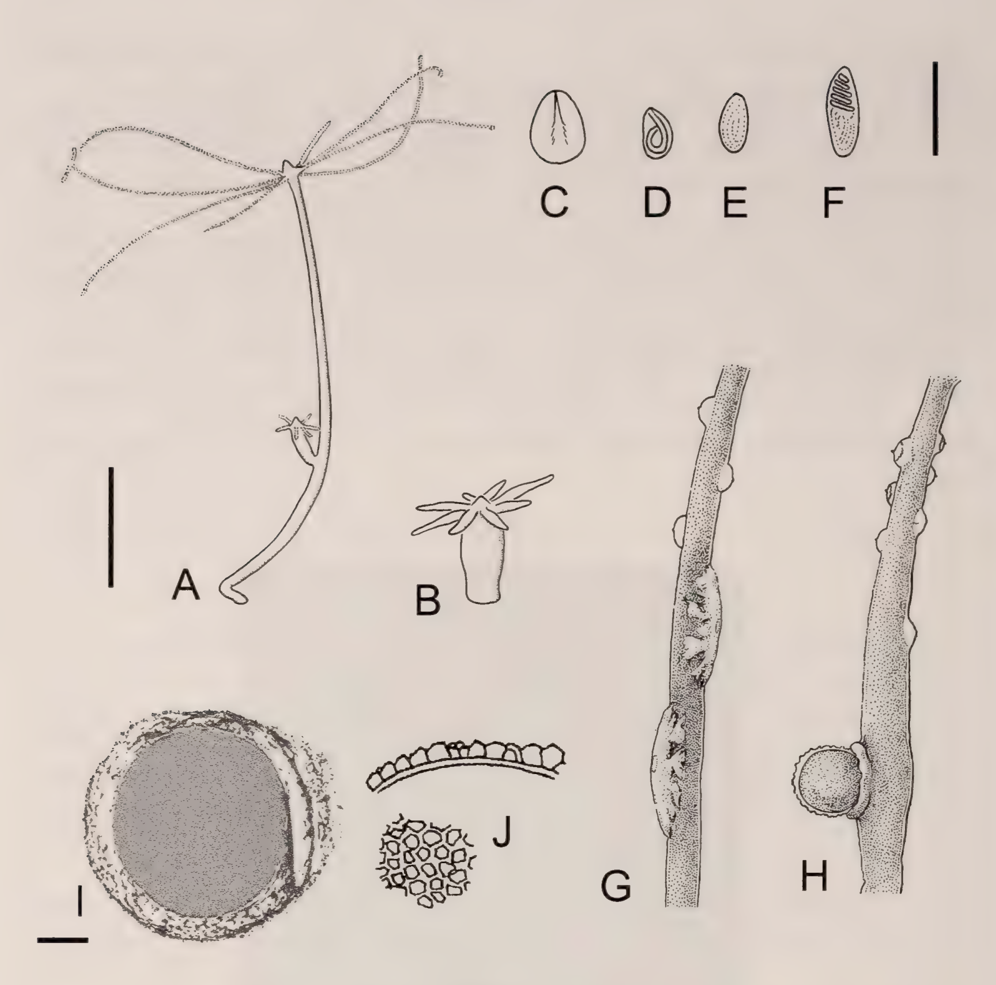


FIG. 47

Hydra viridissima Pallas, 1766. (A) Extended animal with lateral bud, scale bar 2 mm. (B) Contracted polyp, same scale as A. (C-D) Undischarged nematocysts, scale bar 10 μm. (C) Stenotele. (D) Desmoneme. (E) Atrichous isorhiza. (F) Holotrichous isorhiza. (G) Polyp body with two developing oocytes in lower half and three male gonads in upper half; modified from Brien & Reniers-Decoen (1951). (H) Polyp body with encapsulated embryo in lower half and male gonads in upper half; modified from Brien & Reniers-Decoen (1951). (I) Schematic optical section of an encapsulated embryo (embryotheca), on the right side, the side facing originally the mother animal, there is a chamber in the capsule wall; modified after Campbell (1999); scale bar 0.1 mm. (J) Part of embryotheca with polygonal plates, top in a section, below a surface aspect; from Ball (1967).

DESCRIPTION (Holstein, 1995; Campbell, 1999; own observations): Intensively green animals due to symbiotic algae in gastrodermis. Hydranth body cylindrical, thickness depending on state of contraction, no distinct foot region, with flat attachment disk, hypostome conical, below hypostome usually 5-8 tentacles (4-11 possible), tentacles shorter than hydranth body. Contracted hydranths with tentacles arranged around small conical hypostome. Vegetative multiplication by buds, 1-4 tightly

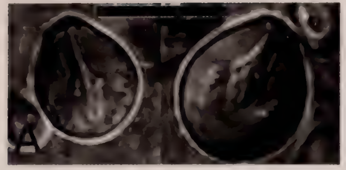





FIG. 48

Hydra viridissima Pallas, 1766; cnidome, intact capsules; scale bar 10 μm. (A) Stenoteles. (B) Desmonemes. (C) Atrichous isorhizas. (D) Holotrichous isorhizas.

clustered in lower third of hydranth body, tentacles of buds formed more or less simultaneously. Sexual reproduction as hermaphrodites, frequently proterandric or simultaneous hermaphrodites, more rarely ovocytes developing before spermatids. Male gonads in distal part below tentacles, usually several, mammiform with a single terminal papilla. Oocyte formation in more proximal region of hydranth body. Fertilized eggs spherical, not attached to the surrounding substrate, perisarc casing (embryotheca) multilayered, with or without polygonal plate pattern, with an extra chamber in the side facing the hydranth.

Nematocysts (Fig. 47C-F, 48A-D):
- stenoteles, ovoid, width/length ratio about 0.78
- desmonemes
- atrichous isorhizas, almond-shaped, smaller than next capsule, more rounded, no distinctly ordered coils of the shaft visible
- holotrichous isorhizas, relatively elongate, sole-shaped, ratio length-width >2, shaft in intact capsule forming four distinct, ordered coils in upper part of capsule (near opening).

DIMENSIONS: Contracted 1-3 mm, fully expanded up to 5-20 mm, embryotheca about 0.4 mm. For nematocyst measurements see Ball (1967), McAuley (1984), Heitkamp (1986), Holstein (1995), or Campbell (1999).

BIOLOGY: A freshwater species often occurring in small, stagnant freshwater ponds with plants. May penetrate into slightly brackish waters (0.5%, Holstein, 1995). The gametogenesis and reproduction was studied in detail by Brien & Reniers-Decoen (1951). The transmission of the zoochlorellae via the eggs was studied by Muscatine & McAuley (1982). For stain and population differences see McAuley (1984).

DISTRIBUTION: Likely cosmopolitan (Heitkamp, 1986), occurs all over Europe, including the British Isles, Iceland, and Scandinavia (Holstein, 1995). Type locality: not specified, but must be Europe.

Hydra circumcincta Schulze, 1914 Figs 49-50

Hydra polypus Linnaeus, 1758: 816. – Brauer, 1909: 792.
Hydra attenuata Pallas, 1766: 32.
Hydra pallens Linnaeus, 1767: 1320.
Hydra braueri Bedot, 1912: 602. – Campbell & Holstein, 1991: 307, synonym.
Hydra circumcincta Schulze, 1914: 396, fig'd. – Tardent *et al.*, 1968: 985, figs 1-5. – Heitkamp, 1986: 537, fig. 5. – Holstein, 1995: 71, figs 8e-h, 25-28. – Campbell, 1989: 238, synonymy. – Stepanjants *et al.*, 2006: 227, fig. 1a.

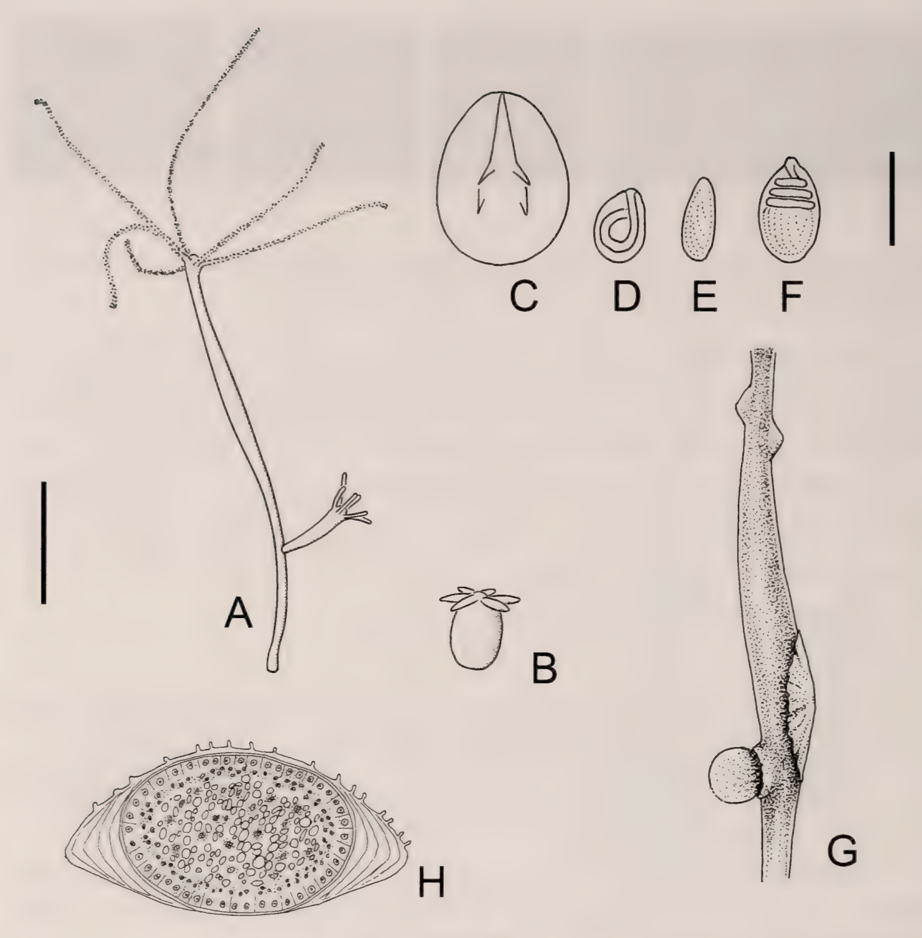


FIG. 49

Hydra circumcincta Schulze, 1914. (A) Extended animal with lateral bud, after life, scale bar 1 mm. (B) Contracted polyp, same scale as A. (C-D) Undischarged nematocysts, scale bar 10 μm. (C) Stenotele. (D) Desmoneme. (E) Atrichous isorhiza. (F) Holotrichous isorhiza. (G) Polyp body with developing oocyte and egg in lower half and two male gonads in upper half; modified from Tardent *et al*. (1968) and Holstein (1995). (H) Cross-section of an encapsulated embryo; from Schulze (1917).

Hydra stellata Schulze, 1914: 396, fig'd. – Tardent *et al*., 1968: 995, synonym. – Ball, 1967: 86.
Hydra ovata Boecker, 1920: 254, fig'd. – Tardent *et al*., 1968: 996, synonym.
Hydra graysoni Maxwell, 1972: 547, figs 1-2. – Holstein, 1995: 74, synonym.

MATERIAL EXAMINED: Switzerland, Wohlensee, 46.961°N 07.374°E, 0 m depth, under stone; one specimen collected 03.05.1997; not preserved, used for DNA extraction. – Switzerland, Lake Geneva, 46.24636°N 06.192282°E, 0.5-1 m depth; several specimens collected 02.09.2007; on algae and plants; not preserved, used for DNA extraction. – Switzerland, near Geneva, La Pleine, train bridge over brook Allondon, 46.179593°N 06.009157°E; depth 0.2 m on plants; several specimens collected 08.09.2007; not preserved, used for DNA extraction.

DIAGNOSIS: Small *Hydra* with short tentacles, no pedicel, holotrichous isorhizas ovoid, ratio length/width <1.5, thread in 3-4 distinct coils in upper part of capsule.

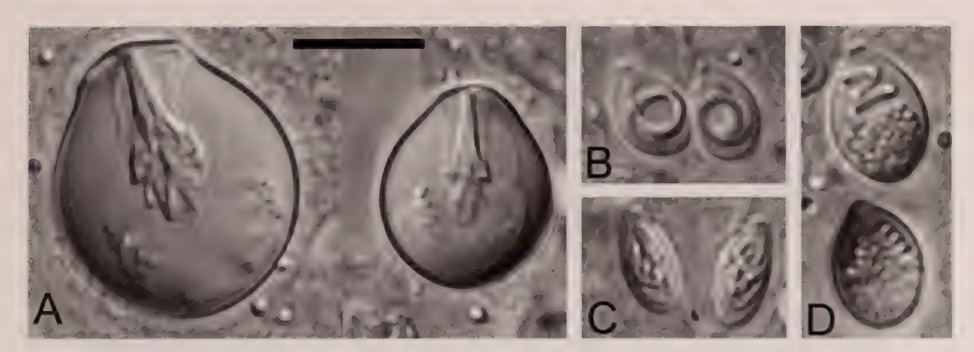


FIG. 50

Hydra circumcincta Schulze, 1914; cnidome, intact capsules; scale bar 10 μm. (A) Stenoteles. (B) Desmonemes. (C) Atrichous isorhizas. (D) Holotrichous isorhizas.

DESCRIPTION (Holstein, 1995; own observations): Small, pale *Hydra*, whitish to light brown-grey, occasionally red due to pigments taken up through food. Hydranth body cylindrical, thickness depending on state of contraction, no distinct foot region, with flat attachment disk, hypostome conical, below hypostome usually six tentacles, sometimes five tentacles, tentacles shorter than hydranth body (ratio < 0.5), held horizontally. Contracted hydranths with star-shaped tentacle crown. Vegetative multiplication by buds, these relatively basal, tentacles of buds formed simultaneously, usually six in number. Vegetative and sexual reproduction can occur simultaneously. Sexual reproduction as hermaphrodites, sometimes proterandric; male gonads like a shallow cone, without terminal papilla, in distal part of body, usually several arranged spirally. Oocyte formation in more proximal region of hydranth body. Fertilized eggs usually attached to leaves or stone, perisarc casing (embryotheca) characteristically flattened (Fig. 49H), underside attached to the substrate, upper side more curved, with a few blunt processes, sometimes slightly capitate (variable).

Nematocysts (Fig. 49C-F, 50A-D):

- stenoteles, ovoid, two size classes, width/length ratio about 0.85
- desmonemes
- atrichous isorhizas, almond-shaped, smaller than next capsule, no distinctly ordered coils of the shaft visible
- holotrichous isorhizas, characteristically ovoid, ratio length/width <1.5, shaft in intact capsule forming 3-4 distinct coils in upper part of capsule (near opening).

DIMENSIONS: Extended polyp 5-15 mm. For nematocyst measurements see Ball (1967), Tardent *et al*. (1968), Holstein (1995), or Stepanjants *et al*. (2006).

BIOLOGY: Rather photophobic, occurs on stones and leaves in shallow waters, much rarer than *H. vulgaris* and *H. oligactis*. Reproductive throughout the year (Holstein, 1995).

DISTRIBUTION: In Europe reaching from northern Italy to polar circle, including the British Isles, not Iceland. Also present outside Europe, e. g. Russia, Japan, North America (Heitkamp, 1986; Holstein, 1995; Stepanjants *et al*., 2006) Type locality: Berlin, Germany.



FIG. 51

Hydra oligactis Pallas, 1766; living animals from Geneva, Switzerland, left with vegetative budding (note characteristic unequal length of tentacles in bud), size about 1 cm, right with developing eggs (note reduction of tentacle length by reproductive exhaustion).

Hydra oligactis Pallas, 1766 Figs 51-53

Hydra oligactis Pallas, 1766: 29. – Semal-Van Gansen, 1954a: 270, figs 2, 8c-d, pl. 2 figs 4-7. – Heitkamp, 1986: 530, fig. 1A-L. – Holstein, 1995: 75, figs 8m-9, 29-34.
Hydra fusca Linnaeus, 1767: 1320. – Brien & Reniers-Decoen, 1949: 295, figs 1-27. – Brien, 1965: 1, figs 1-48, 55-74.
Hydra roeselii Haacke, 1879: 622.
Hydra rhaetica Asper, 1880a: 205, figs 2-3.
Hydra rhistica Asper, 1880b: 139.
? *Hydra monoecia* Downing, 1900: 228.
? *Hydra pallida* Beardsley, 1904: 160.
? *Hydra corala* Elrod & Ricker, 1902: 258.
? *Hydra dioecia* Downing, 1905: 382, pls 22-24.
Pelmatohydra oligactis. – Schulze, 1914: 57, figs 57-72.

MATERIAL EXAMINED: Switzerland, Bern, Moossee, 47.020°N 07.486°E; collected 01.05.1997 on stones, algae, and plants; not preserved, used for nematocyst examinations and DNA extraction; 16S sequence **FN687555**. – Switzerland, Lake Geneva, Port de la Pointe à la Bise, 46.24636°N 06.192282°E; 1 m depth; collected 02.09.2007; infertile; not preserved, used

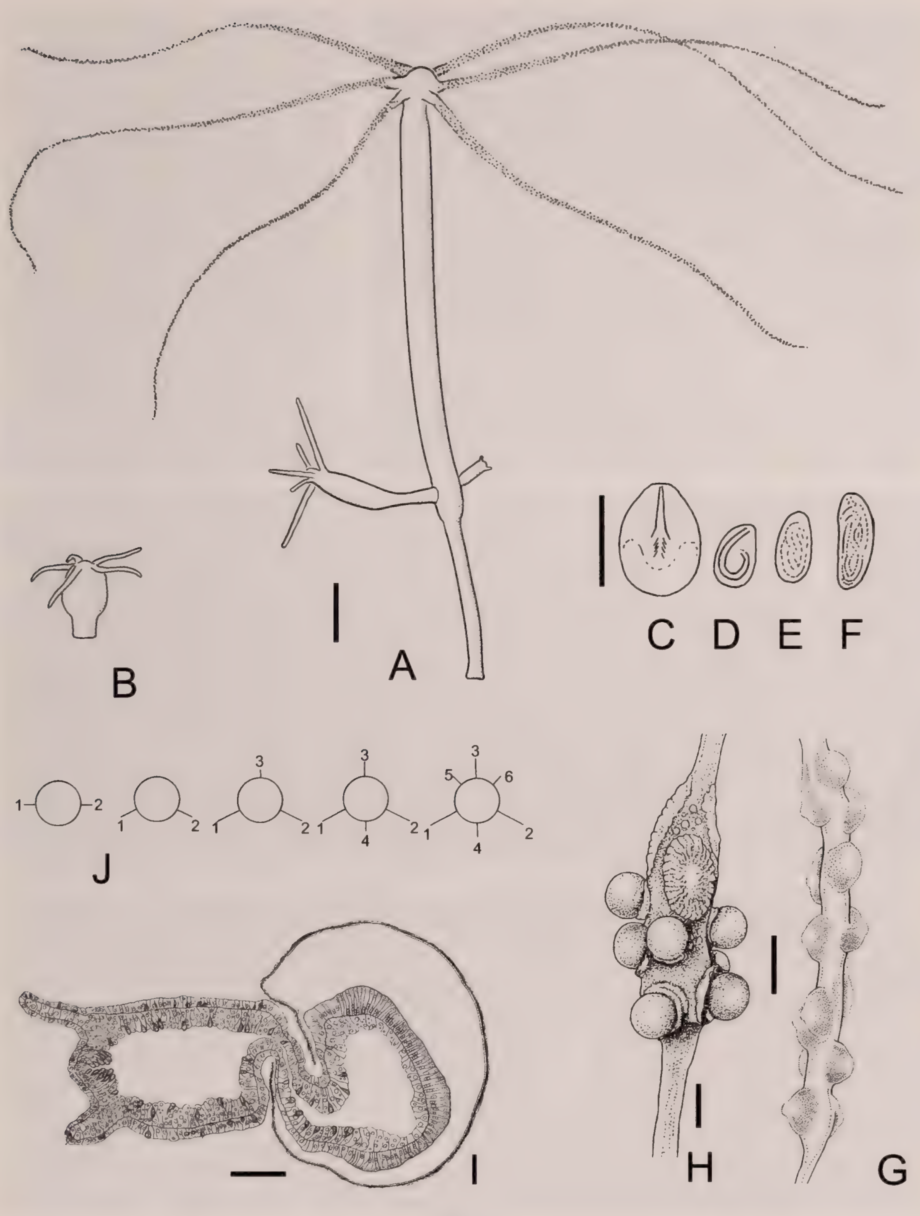


FIG. 52

Hydra oligactis Pallas, 1766. (A) Extended animal with lateral buds, after life, scale bar 1 mm. (B) Contracted polyp, same scale as A. (C-D) Undischarged nematocysts, scale bar 10 μm. (C) Stenotele. (D) Desmoneme. (E) Atrichous isorhiza. (F) Holotrichous isorhiza. (G) Polyp body with male gonads, scale bar 1 mm; modified after Brien (1965) (H) Body of female polyp with developing (top) and mature (below) ovocytes; modified after Brien & Reniers-Decoen (1949). (I) Longitudinal section of a young polyp hatching from its embryotheca, scale bar 0.1 mm; modified after Brien (1965). (J) Sequence of tentacle development in a polyp bud, the numbers identify the consecutively developing tentacles; modified after Schulze (1917).

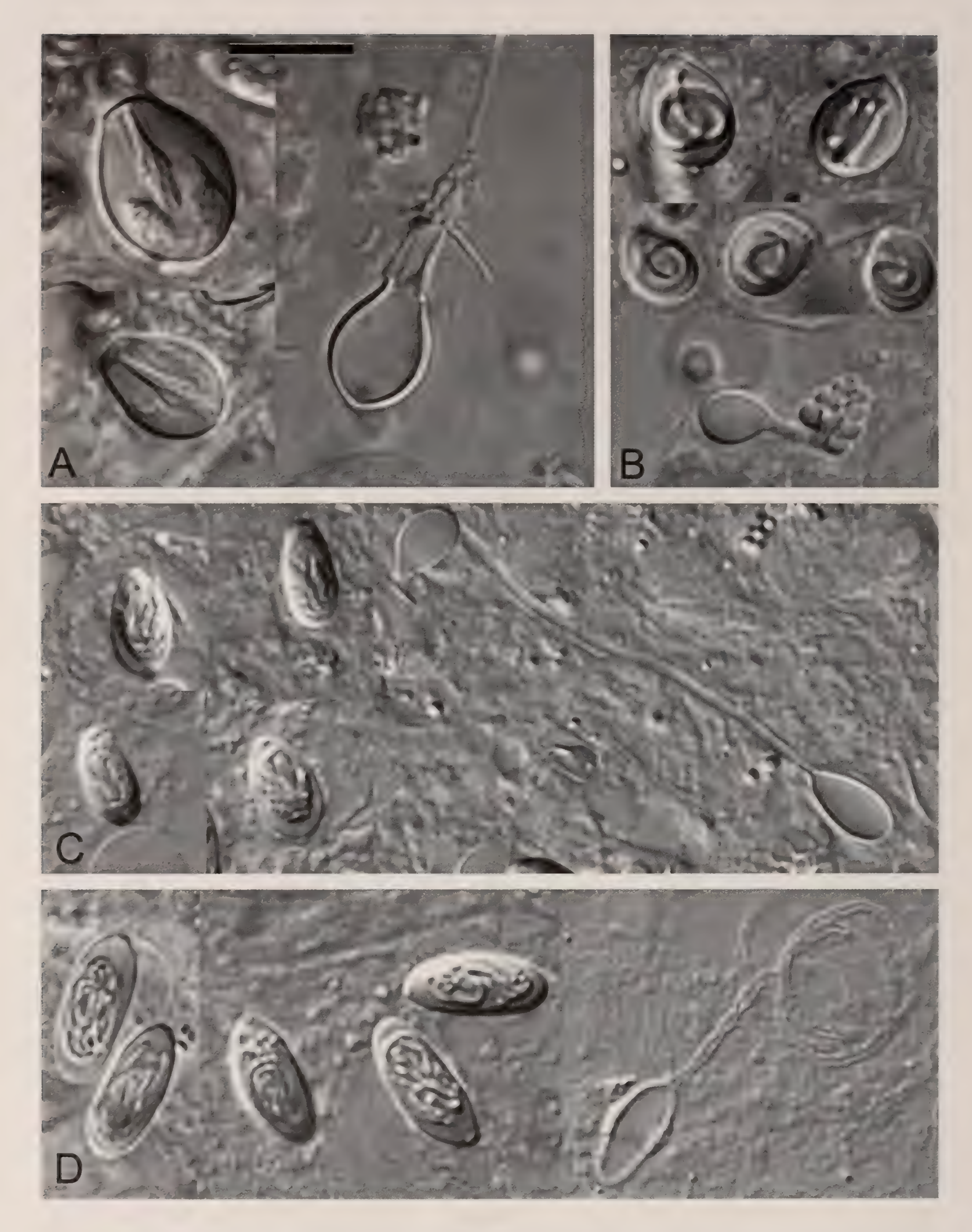


FIG. 53

Hydra oligactis Pallas, 1766; cnidome, intact and discharged capsules; scale bar 10 μm. (A) Stenoteles. (B) Desmonemes. (C) Atrichous isorhizas. (D) Holotrichous isorhizas.

for nematocyst examinations and DNA extraction. – Switzerland, canton of Geneva, La Plaine, train bridge over river Allondon, 46.179593°N 06.009157°E; collected 08.09.2007 on plants; infertile; infertile; not preserved, used for nematocyst examinations and DNA extraction. – Norway, Espeland near Bergen, 60.275728°N 05.244598°E; collected 20.09.2008, on *Spyrogyra*

and plants; infertile; not preserved, used for nematocyst examinations and DNA extraction. – MHNG INVE 67086; Switzerland, canton of Genève, L'Avenir, small brook named Paradis; 46.224°N 06.241°E; 0.2 m depth; collected 14.11.2009; 10 animals on *Elodea*, some reproductive females.

Diagnosis: Large *Hydra* with long tentacles, with more or less distinct pedicel, holotrichous isorhizas elongated, ratio length/width about 2, thread inside capsule only in irregular coils.

Description (Holstein, 1995; own data): Large *Hydra*, colour typically light-brown but depending on food, may also be black-brown, bright-orange, intensively red, or greenish (but without algal symbionts). Hydranth body cylindrical, thickness depending on state of contraction, with macroscopically and histologically clearly separable pedicel, pedicel thinner and more transparent than rest of body, length depending on age, temperature, and food availability, hypostome dome-shaped, 4-6 tentacles, length variable and depending on health of animal, reaching lengths of 2-6 times the body length, in upright animals drooping parallel to body, tentacles in totally contracted animals not star-like, remaining curved.

Vegetative multiplication by buds, budding zone just above distal end of pedicel, buds arranged in a tight spiral, up to six buds per animal, developing tentacles of buds of unequal length, developing in an ordered sequence, first pair of tentacles develop as an opposite pair, later developing ones are intercalated, remaining shorter during until all tentacles reach their full length (Fig. 52J).

Sexes strictly separate, no sex change, onset of gametogenesis stops vegetative budding, body size and tentacles become reduced in sexually reproducing animals; males with up to 30 gonads, hemispherical, with or without distal papilla, papilla when present rather broad. Female animals develop several spherical eggs in middle region of body. Embryotheca very thin, smooth or with variable, shallow processes, surface more wavy than spiny.

Nematocysts (Figs 52C-F, 53A-D):

- stenoteles, ovoid, sizes very variable, width/length ratio about 0.73
- desmonemes
- atrichous isorhizas, smaller than holotrichous capsule, thread with irregular coiling
- oblong holotrichous isorhizas, thread coiled irregularly.

Dimensions: Second-largest *Hydra* of the European fauna, height of body usually around 10 mm, may reach 30 mm. Extreme tentacle length of 25 cm have been reported. Egg size about 1 mm. For nematocyst measurements see Holstein (1995).

Biology: *Hydra oligactis* is a stenothermal species (max. 28°C) occurring on the underside of stones and water plants along the shore-line of large, productive lakes. Also in flowing water bodies with rocky bottom and mountain lakes, but in not small, stagnant ponds. The latter biotope is more characteristic for *H. viridissima*, which prefers higher temperatures. In nature, sexual reproduction takes place in autumn (lowlands) or summer (alpine lakes). Sexual reproduction can be induced in culture by lowering the temperature from 18-20°C to 10-12°C (Holstein, 1995).

For details on sexual reproduction, gametogenesis, embryology, and senescence see Brien & Reniers-Decoen (1949) and Brien (1965). *Hydra oligactis* is a popular

laboratory animal and one of the best investigated hydroids. There is a vast body of literature on experimental biology and ecology of *Hydra oligactis* which cannot be treated here.

DISTRIBUTION: Widespread and common on the entire European continent, including the British Isles and Iceland, also Russia and North America (Hyman, 1930; Holstein, 1995; Stepanjants *et al.*, 2006). Type locality: Europe.

Hydra vulgaris **Pallas, 1766** Figs 54-55

Hydra vulgaris Pallas, 1766: 30. – Heitkamp, 1986: 540, fig. 7. – Holstein, 1995: 82, figs 38-42.
Hydra grisea Linnaeus, 1767: 1320.
Hydra vulgaris aurantiaca Ehrenberg, 1838: 115, pl. 2 figs 1-3.
Hydra trembleyi Haacke, 1879: 622.
Hydra attenuata. – Schulze, 1914: 398, fig'd. – Schulze, 1917: 60, figs 26-47. – Semal-Van Gansen, 1954a: 270, figs 1, 4a-b, 7, 8a-b, pl. 1 figs 1-6, pl. 2 figs 1-2. – Semal-Van Gansen, 1954b: 187, figs 1-3. – Heitkamp, 1986: 539, fig. 6. – Brien & Reniers-Decoen, 1952: 285, figs 1-17. – Brien, 1965: 67, figs 49-53. [not *H. attenuata* Pallas, 1766 = *Hydra circumcincta* Schulze, 1914]

MATERIAL EXAMINED: Switzerland, Wohlensee, 46.961°N 7.374°E; 0.2 m depth; collected 03.05.1997; one infertile animal; not preserved, used for nematocyst examinations and DNA extraction. – Switzerland; canton of Geneva, pond south of La Renfile, 46.221133°N 06.28043°E; 0.2 m depth; collected 03.11.2003; few infertile animals; not preserved, used for nematocyst examinations and DNA extraction. – Switzerland, canton of Geneva, pond south of La Renfile, 46.221°N 06.28043°E; 0.2 m depth; collected 14.06.2008; few infertile animals; not preserved, used for nematocyst examinations and DNA extraction. – Switzerland; canton of Geneva, pond south of La Renfile; 0.2 m depth; collected 14.06.2008; on *Phragmites*; several animals, some with male gonads; not preserved, used for nematocyst examinations and DNA extraction. – France; Haute Savoie, Lac de Machilly, 46.256129°N 06.326323°E; 0.2 m depth; collected 25.08.2007; few infertile animals; not preserved, used for nematocyst examinations and DNA extraction. – Norway; Norway, Espeland, 60.275728°N 5.244598°E; 0.2 m depth; collected 20.09.2208; on *Spirogyra* and plants plants; few infertile animals; not preserved.

DIAGNOSIS: Medium sized *Hydra* with long tentacles, without algal symbionts, no or indistinct pedicel, holotrichous isorhizas oblong, ratio length/width >2, thread in 4-5 oblique or transverse coils in upper part of capsule, stenotele width/length ratio about 0.78.

DESCRIPTION: (Holstein, 1995; own observations): Small, brown-ochre coloured *Hydra*. Hydranth body cylindrical, thickness depending on state of contraction, diameter increasing continuously from tentacles towards basal, reaching a maximum in the budding zone, then decreasing slightly again, no distinct pedicel region but basal region usually more transparent and thinner, with flat attachment disk, hypostome conical, below hypostome 6-8 tentacles, tentacles may be longer than hydranth body when fully extended, about half as long when contracted, length of tentacles depends on food supply and environmental factors.

Vegetative multiplication by buds, these in lower third of body, usually only 1-2 buds, rarely 3-4, initial four tentacles of buds formed more or less simultaneously, later more tentacles develop and thus tentacles transiently of unequal length. Vegetative and sexual reproduction can occur simultaneously. Sexual reproduction gonochoristic, hermaphroditic animals very rare. Male gonads hemispherical and with terminal papilla, developing in part of body above budding zone, up to 20 possible.

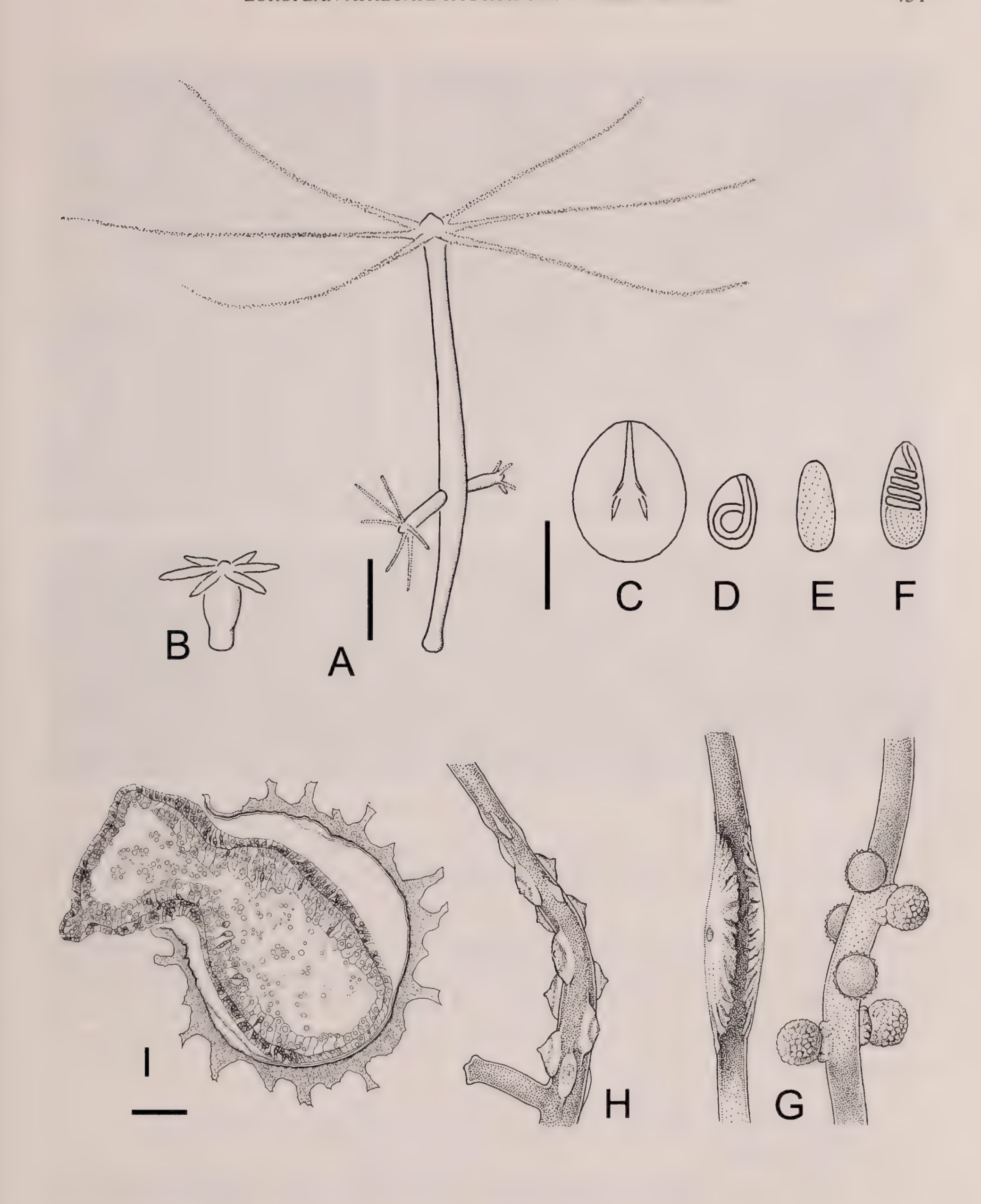


FIG. 54

Hydra vulgaris Pallas, 1766. (A) Extended animal with lateral buds, after life; scale bar 1 mm. (B) Contracted polyp, same scale as A. (C-D) Undischarged nematocysts, scale bar 10 μm. (C) Stenotele. (D) Desmoneme. (E) Atrichous isorhiza. (F) Holotrichous isorhiza. (G) Polyp bodies with developing oocytes (left) and fertilized, encapsulated eggs (right); modified from Brien & Reniers-Decoen (1951). (H) Polyp body with with male gonads; modified from Brien & Reniers-Decoen (1951). (I) Longitudinal section of a young polyp hatching from its embryotheca, note the spines of the capsule; scale bar 0.1 mm; modified after Brien (1965).

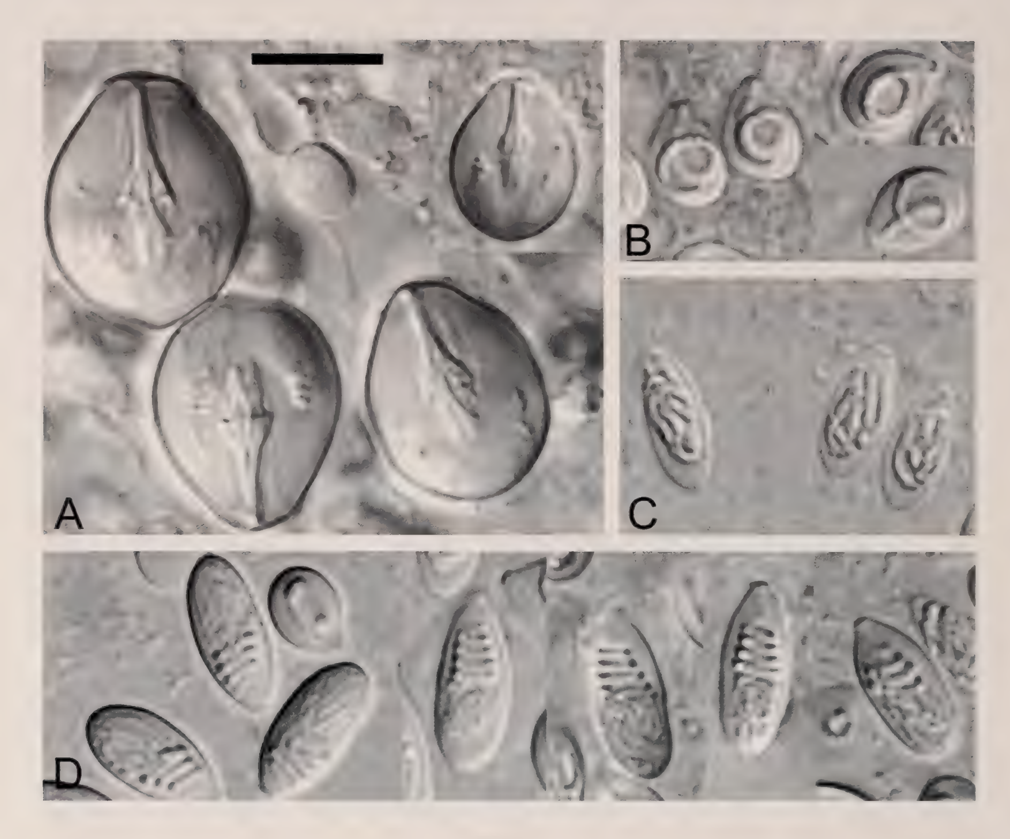


FIG. 55

Hydra vulgaris Pallas, 1766; cnidome, undischarged capsules; scale bar 10 μm. (A) Stenoteles. (B) Desmonemes. (C) Atrichous isorhizas. (D) Holotrichous isorhizas.

Oocyte formation in middle region of hydranth body, up to 6-8 white eggs, fertilized eggs usually remain attached to mother animal, perisarc casing (embryotheca) with spines (Fig. 54I), often bifurcated, but shape and length very variable and depending on environmental influences. In hermaphrodites, male and female gonads mixed, not in separate regions.

Nematocysts relatively large (Fig. 54C-F, 55A-D):

- stenoteles, ovoid, two size classes, width/length ratio about 0.78
- desmonemes
- atrichous isorhizas, almond-shaped, smaller than next capsule, no distinctly ordered coils of the shaft visible
- holotrichous isorhizas, oval, ratio length/width > 2, shaft in intact capsule thread in 4-5 oblique or transverse coils in upper part of capsule, coiling somewhat variable even within a single animal.

DIMENSIONS: Extended hydranth usually 3-6 mm, may reach sizes of up to 15 mm. Egg size about 1 mm. For nematocyst measurements see Semal-Van Gansen (1954b) and Holstein (1995).

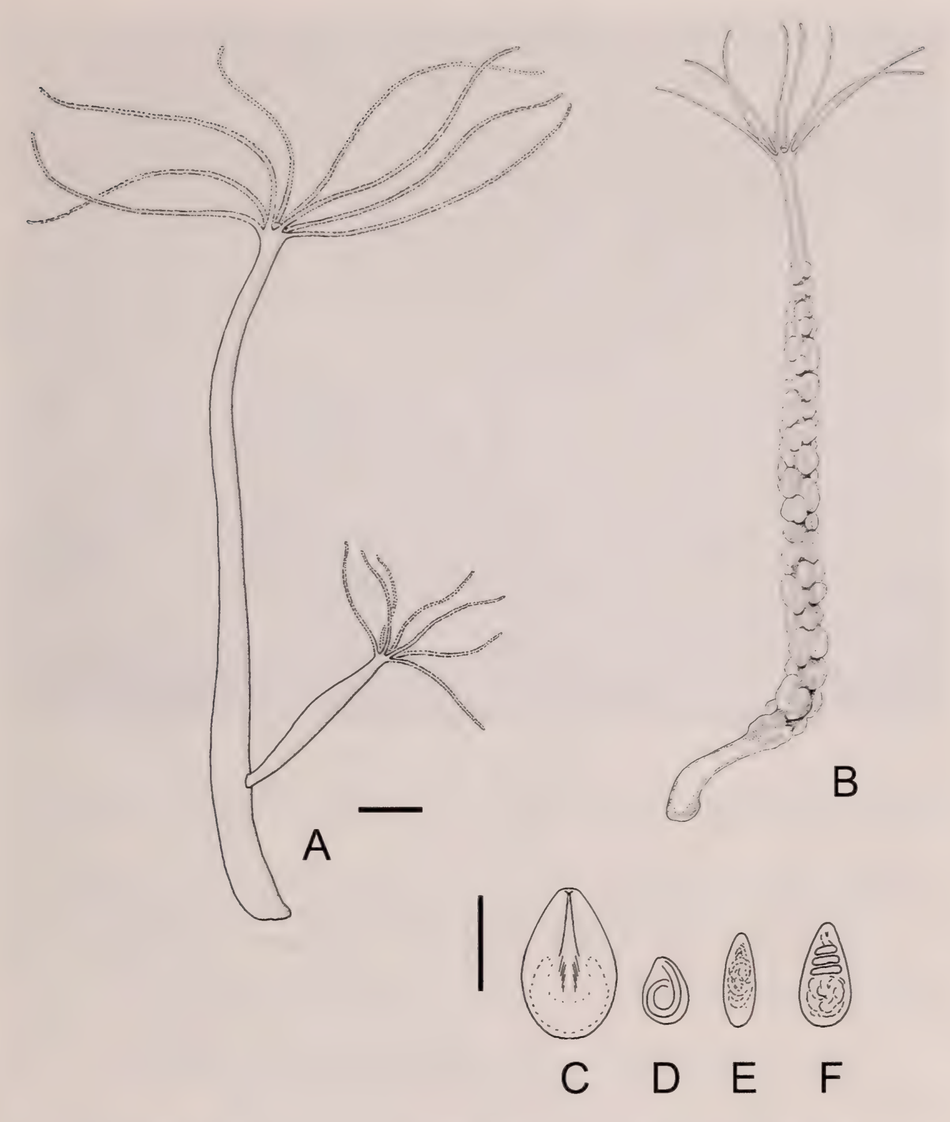


FIG. 56

Hydra oxycnida Schulze, 1914. (A) Extended animal with lateral bud, note relatively low budding site; scale bar 1 mm; modified after Brien (1961, as *H. pirardi*). (B) Animal with male gonads; modified after Brien (1961, as *H. pirardi*). (C-D) Undischarged nematocysts, scale bar 10 μm. (C) Stenotele. (D) Desmoneme. (E) Atrichous isorhiza. (F) Holotrichous isorhiza.

BIOLOGY: A eurythermal species (7-29°, Holstein, 1995). For a study of gametogenesis and development see Brien & Reniers-Decoen (1952) and Brien (1965). For sex determination and hermaphrodites see Tardent (1968).

DISTRIBUTION: Entire European continent and British Isles. Type locality: Europe (Pallas, 1766).



FIG. 57

Hydra oxycnida Schulze, 1914; nematocysts, mostly stenoteles, living tissues; photo courtesy Daniel Martinez, Pomona College, CA, USA.

Hydra oxycnida Schulze, 1914 Figs 56-57

Hydra oxycnida Schulze, 1914: 396, fig'd. – Schulze, 1917: 83, figs 53-56. – Boecker, 1921: 97, fig'd. – Schulze, 1951: 925. – Heitkamp, 1986: 534, fig. 3. – Holstein, 1995: 79, figs 8a-d, 35-37.

Hydra oxycnidoides Schulze, 1927: 131, figs 2-3. – Holstein, 1995: 82, synoynym.

Hydra pirardi Brien, 1961: 304, figs 1-40, pls 1-2. – Holstein, 1995: 82, synoynym.

DIAGNOSIS: Very large, dark brown *Hydra* without pedicel, stenoteles markedly ovoid, width/length ratio 0.6, upper part characteristically pointed.

DESCRIPTION (Holstein, 1995): Very large *Hydra* species, body dark pigmented, without pedicel but basal region more transparent, diameter largest near base, then continuously decreasing towards above up to tentacle whorl, tentacles 7-8, rarely 6-11, relatively short, extended reaching only 1/4 to 1/3 of body length, polyp buds form tentacles simultaneously.

Vegetative multiplication by buds, budding zone relatively basal, buds arranged in one whorl, tentacles of buds develop simultaneously, thus all of equal length.

Sexes strictly separate, no sex change, onset of gametogenesis stops vegetative budding and nematocyst production; male gonads arranged irregularly along body, hemispherical, without distal papilla; female animals develop several spherical eggs. Embryotheca not reliably known.

Nematocysts relatively large (Fig. 56C-F):
- stenoteles of variable sizes, quite slender, width/length ratio 0.6, upper part relatively pointed (Fig. 57)
- desmonemes
- atrichous isorhizas, almond-shaped, about as long as next capsule, no distinctly ordered coils of the shaft visible
- holotrichous isorhizas, ovoid to oval, ratio length/width >2, shaft in intact capsule thread in 3-4 oblique or transverse coils in upper part of capsule.

DIMENSIONS: Largest *Hydra* species with a body column of 20-30 mm. For nematocyst measurements see Brien (1961) or Holstein (1995).

BIOLOGY (Holstein, 1995): Occurs in waters with a slow current. Lowering the temperature from 19°C to 8°C induces gametogenesis, reproductive season is thus in late autumn. Sexual reproduction causes a strong reduction of tentacle length and body size.

DISTRIBUTION: A northern European species, occurring from Belgium, Holland, northern Germany, Finland, and Russia. Also Lake Baikal (Holstein, 1995). Type locality: Berlin, Germany.

CLADE CAPITATA SENSU STRICTO

FAMILY MOERISIIDAE POCHE, 1914

DIAGNOSIS: Hydroid with moniliform or modified moniliform tentacles, scattered or in one whorl around middle part of the hydranth body; gonophores between or just under the tentacles; polyp buds develop in lower part of hydranth; hydrocaulus base ending in podocysts, or with short stolon-like tubes ending in podocysts or hydranths.

Gonophores released as medusa with prismatic manubrium extending into long, basal perradial lobes; no gastric peduncle; mouth simple, cruciform; gonads on manubrium and manubrial lobes; with four or more tentacles, hollow, with adnate bulbs; with abaxial ocelli; no statocysts.

KEY TO THE GENERA

1a polyp tentacles hollow, irregularly moniliform, medusa tentacles moniliform . . . . *Moerisia*
1b polyp tentacles solid, with a larger terminal nematocyst cluster and smaller clusters on upper side of tentacles, medusa tentacles with nematocyst clusters in clasps and not rings . . . . *Odessia*

Genus ***Moerisia*** Boulenger, 1908

Moerisia Boulenger, 1908; type species *Moerisia lyonsi* Boulenger, 1908 by monotypy.
Annulella Ritchie, 1915; type species *Annulella gemmata* Ritchie, 1915 by monotypy.
Ostroumovia Hadzi, 1928; type species *Moerisia inkermanica* Paltschikowa-Ostroumowa, 1925 by monotypy.
Caspionema Derzhavin, 1912; type species *Caspionema pallasi* Derzhavin, 1912 by monotypy.

DIAGNOSIS: Moerisiidae with polyps having hollow, irregularly moniliform tentacles, medusa tentacles moniliform.

REMARKS: The status of several nominal *Moerisia* species is not entirely clear and some might turn out to be conspecific. Only one *Moerisia* species, namely *M. inkermanica*, is known to occur in Europe. Within the region of covered by the ERMS (Costello *et al.*, 2001), there is additionally *Moerisia carine* Bouillon, 1978b, which has been recorded off Lebanon (Goy *et al.*, 1991). It is characterized by a medusa with very short manubrial pouches, up to 16 tentacles, and globular tentacular bulbs. For more details see Bouillon *et al.* (2004). *Moerisia pallasi* (Derzhavin, 1912), endemic to Caspian Sea, resembles *M. inkermanica* and both could be conspecific. *Moerisia lyonsi* Boulenger, 1908 is known from an inland lake in Egypt (Lake Qurun, Boulenger, 1908) and also from America (Calder & Burrell, 1967). It does not occur in the Mediterranean as suggested by Bouillon *et al.* (2004). Its medusa usually has only four tentacles (exceptionally more in 14% of 400 animals) and the hydroid does not form podocysts. For more details see Bouillon *et al.* (2004).

KEY TO SPECIES OF *MOERISIA* OF THE ERMS ZONE

1a gonads on very long perradial basal extension of manubrium, up 32 tentacles . . . . *M. inkermanica*
1b very short manubrial pouches, up to 16 tentacles . . . . *M. carine*

Moerisia inkermanica Paltschikowa-Ostroumowa, 1925 Fig. 58

Moerisia inkermanica Paltschikowa-Ostroumowa, 1925: 273, figs 1-3. – Valkanov, 1953: 46, figs 3-9. – Bouillon *et al.*, 2004: 82, fig. 46A. – Petersen, 1990: 125. – Nogueira & De Oliveira, 2006: 36, figs 1-5.
? not *Annulella gemmata* Ritchie, 1915: 541, text figures, pls 30-30a. – Rees & Thursfield, 1965: 38, synonym. – Petersen, 1990: 126, fig. 4, valid.
? *Caspionema pallasi* Derzhavin, 1912: 390, figs 1-5.
Annulella gemmata. – Rioja, 1924: 213, figs 1-5.
Ostroumovia inkermanica. – Hadzi, 1928: 39. – Kramp & Paspaleff, 1938: 27, figs part II 1-17. – Paspaleff, 1938: 27, figs 1-17. – Kramp, 1938a: 103, fig. 1. – Kramp, 1938b: 45, figs 1-5, plate. – Kramp, 1958: 364. – Kramp, 1961: 216. – Rees & Thursfield, 1965: 38. – Rees, 1958: 543. – Kramp, 1959: 171, fig. 234. – Saraber, 1962: 117, fig. – Bouillon *et al.*, 1969: 75, fig. – Millard, 1975: 466, fig. 142A-G.

MATERIAL EXAMINED: IRSNB, as *Ostroumovia inkermanica*; IG 27838, collection of J. Bouillon; France, Normandy, Canal de Caen; several polyps with medusa buds, growing on piece of reed; 5 mature medusae from plankton.

DIAGNOSIS: Moerisiid medusa with less than 32 tentacles, nematocyst on tentacles in regular rings; gonads on very long perradial basal extension of manubrium. Polyps solitary, with hollow moniliform tentacles, medusa buds below tentacles, one or more podocysts at base.

DESCRIPTION (after examined material; Paltschikowa-Ostroumowa, 1925; Paspaleff, 1938; Kramp, 1958): Polyps solitary but may be aggregated into groups, very contractile, relaxed polyp subdivided into four regions: basal attachment discs, pedicel, hydranth body, and hypostome. Base of polyp ending in one or more pedal discs adhering to substrate, attachment disc a shallow plano-convex perisarc capsule. Sometimes base of polyp issuing thin, stolon-like processes that can be branched, usually ending in pedal disc or podocysts (Fig. 58H). Pedicel of mature polyp comprises about ½ of total height, with large gastrodermal cells, lumen narrowed.

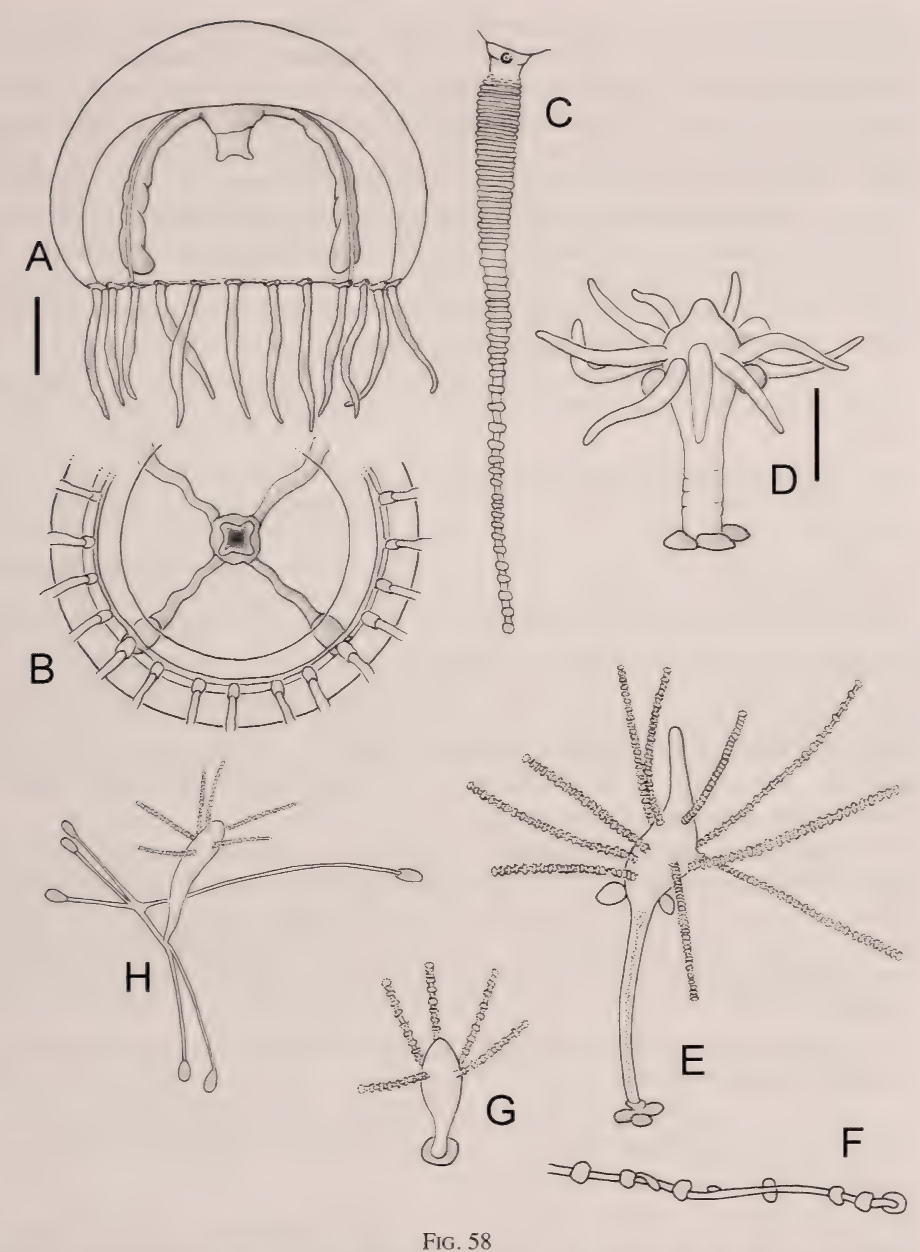


FIG. 58

Moerisia inkermanica Paltschikowa-Ostroumowa, 1925. (A) Schematic diagram of side view of mature a medusa, tentacles contracted, scale bar 1 mm. (B) Oral view of medusa. (C) Single tentacle of medusa, partially extended, note regular rings of nematocyst clusters (moniliform tentacle). (D) Contracted polyp with medusa buds, scale bar 0.5 mm. (E) Polyp with extended tentacles. (F) Part of completely extended polyp tentacles, note moniliform arrangement of nematocyst clusters. (G) Young polyp. (H) Polyp that had lost its basal part with the pedal disc and that formed cysts on long, thin extensions. A-B, D, after preserved material from Normandy; C after Kramp (1938); E-H, after Paspaleff (1938).

Hydranth body about 2-3 times as thick as pedicel, rounded, with middle region bearing tentacles. 8-12 (max. 18) tentacles in two close whorls or scattered, hollow in proximal part, slender, contractile, expanded as long as polyp high, length variable (growth stages), nematocysts concentrated in more or less regular rings (more irregular in younger animals), contracted tentacles appear filiform (Fig. 58D). Hypostome elongated, proboscis-like, contractile, can be elongated to about the same length as hydranth body height, mouth region without concentration of nematocysts. Medusa buds below tentacles near junction to pedicel. Asexual reproduction of the polyp via budding of sister polyps on hydranth body and pedicel, or via production of podocysts that get separated from the polyp. Nematocyst: stenoteles, desmonemes, mastigophores, ? haplonemes. Colours: reddish pigments in gastrodermis.

Newly liberated medusa with four tentacles, tentacular nematocyst clusters not in rings, with ocelli, manubrium tubular and short, exumbrella scattered with nematocysts.

Adult medusa bell-shaped, slightly wider than high, jelly very thick (1/3 to 1/2 of total height). Manubrium composed of a central cylindrical part and long perradial basal lobes. Central tube (stomach) short (1/8 to 1/5 of subumbrellar height) square to cruciform in section, mouth cruciform, margin simple, beset with nematocysts. Perradial stomach lobes extending along 9/10 of subumbrella radius, height only about 1/3 of total manubrium height, distal end often slightly swollen and pendant. Gonads on perradial lobes of manubrium and on interradial walls of stomach. Four radial canals rather short as issued from stomach lobes, thin, ring canal thin. Tentacles 24-32, when contracted shorter than bell height, length variable, tapering; flat marginal bulb, adnate and clasping bell margin, with short abaxial spur containing red ocellus. Tentacular nematocysts concentrated into very regular rings (moniliform), gastrodermis hollow. Nematocysts: like polyp.

Dimensions: Fully grown polyps when contracted about 1 mm, up to 5 mm when expanded (Paspaleff, 1938). Paltschikowa-Ostroumowa (1925) saw polyps extend to a length of 44 mm, but which were considered by Paspaleff (1938) as abnormal. Newly liberated medusa about 0.7 mm (Paltschikowa-Ostroumowa, 1925). Fully grown medusa up to 5.5 mm high and 6.5 mm wide (Kramp, 1938), usually 4-6 mm wide.

Other data: Kramp (1938b) gives a table with the correlation of the medusa size and its tentacle number.

Biology: Occurs usually in brackish waters of shallow depths. The polyps can tolerate 0.5-4% salinity and temperatures from 0-30°C (Paspaleff, 1938). They grow on reeds, pilings, and among polychaete tubes.

Distribution: Black Sea (Paltschikowa-Ostroumowa, 1925; Kramp & Paspaleff, 1938); western Mediterranean (Brinckmann-Voss, 1987; Rioja, 1924, as *Annulella gemmata*); Holland (Saraber, 1962); France (Bouillon *et al.*, 1969); India (Kramp, 1958); South Africa (Millard, 1975); Brazil (Paranaguá, 1966; Nogueira & De Oliveira, 2006); ? Argentina (Zamponi, 1983; but see Genzano *et al.*, 2008). Type locality: Bay of Sevastopol, Black Sea.

Remarks: When describing the mature medusa, Kramp (1938b) claimed to have seen very small statocysts near the bell margin. This was contested by Valkanov

(1953). He re-examined Kramp's serial sections and also gives photographs and a figure of them. He concluded that what Kramp took for a tiny statocyst was in fact a nematocyst capsule in a region of loosened tissue. Furthermore, neither he nor Kramp could find statocysts in new material of *M. inkermanica*. Also subsequent authors (e. g. Rees, 1958, Bouillon, 1985a) regarded Kramp's interpretation as wrong. Saraber (1962), however, mentions small, internal statocysts, although it is not clear whether he had really observed them or only repeated Kramp's earlier interpretation.

Rees & Thursfield (1965) regarded *Annulella gemmata* Ritchie, 1915 as a synonym of *Moerisia inkermanica* Paltschikowa-Ostroumowa, 1925. Millard (1975) thought that they are distinct and also Petersen (1990: 126, fig. 4) kept *Moerisia gemmata* (Ritchie, 1915) as distinct. The polyp depicted by Rioja (1924) as *Annulella gemmata* appears identical to *M. inkermanica* as described here. For biogeographical reasons it more likely belongs to *M. inkermanica*, if the latter species is regarded as distinct from *M. gemmata*.

Caspionema pallasi Derzhavin, 1912 from the Caspian Sea could be conspecific with *Moerisia inkermanica*.

Moerisia carine Bouillon, 1978b

Moerisia carine Bouillon, 1978b: 269, fig. 12. – Goy *et al.*, 1991: 117, fig. 44. – Bouillon *et al.*, 2004: 82, fig. 46A.

DIAGNOSIS: *Moerisia* medusa with very short basal stomach-pouches, up to 16 tentacles, tentacular bulbs globular.

DISTRIBUTION: Papua New Guinea and eastern Mediterranean. Type locality: Laing Island, Papua New Guinea.

REMARKS: This species does not occur along European coasts, but has been recorded near Lebanon (Goy *et al.*, 1991), thus within the region covered by the ERMS (Costello *et al.*, 2001). For a description and figures see Bouillon *et al.* (2004).

Genus ***Odessia*** Paspalew, 1937

Pontia Paspalew, 1936, invalid junior synonym of *Pontia Fabricius* [Lepidoptera] and others.
Odessia Paspalew, 1937; type species *Thaumantias maeotica* Ostroumoff, 1896 by monotypy.

DIAGNOSIS: Moerisiidae with polyps having tentacles with a larger teminal nematocyst cluster and smaller clusters on upper side of tentacles (semimoniliform), medusa tentacles with nematocyst clusters in clasps and not rings.

REMARKS: Only *Odessia maeotica* (Ostroumoff, 1896) occurs in the ERMS region.

Odessia maeotica (Ostroumoff, 1896) Figs 59-63

Thaumantias maeotica Ostroumoff, 1896: 398, pl. 1 figs 2, 4, 5. – Mayer, 1910: 200, fig. 103.
Thaumantias hemisphaerica. – Neppi & Stiasny, 1913: 36, pl. 3 fig. 26. [not *Clytia hemisphaerica* (Linnaeus, 1767)]
? *Caspionema pallasi* Derzhavin, 1912: 390, figs 1-5.
Moerisia gallica Hartlaub, 1917: 417.
Pontia ostroumowi Paspalew, 1936: 28, figs 4-29, pl. 1.
Odessia maeotica. – Paspalew, 1937: 112. – Kramp, 1959: 171, fig. 242. – Kramp, 1961: 215. – Morri, 1981: 36, fig. 9. – Petersen, 1990: 125. – Bouillon *et al.*, 2004: 83, fig. 46H-I.

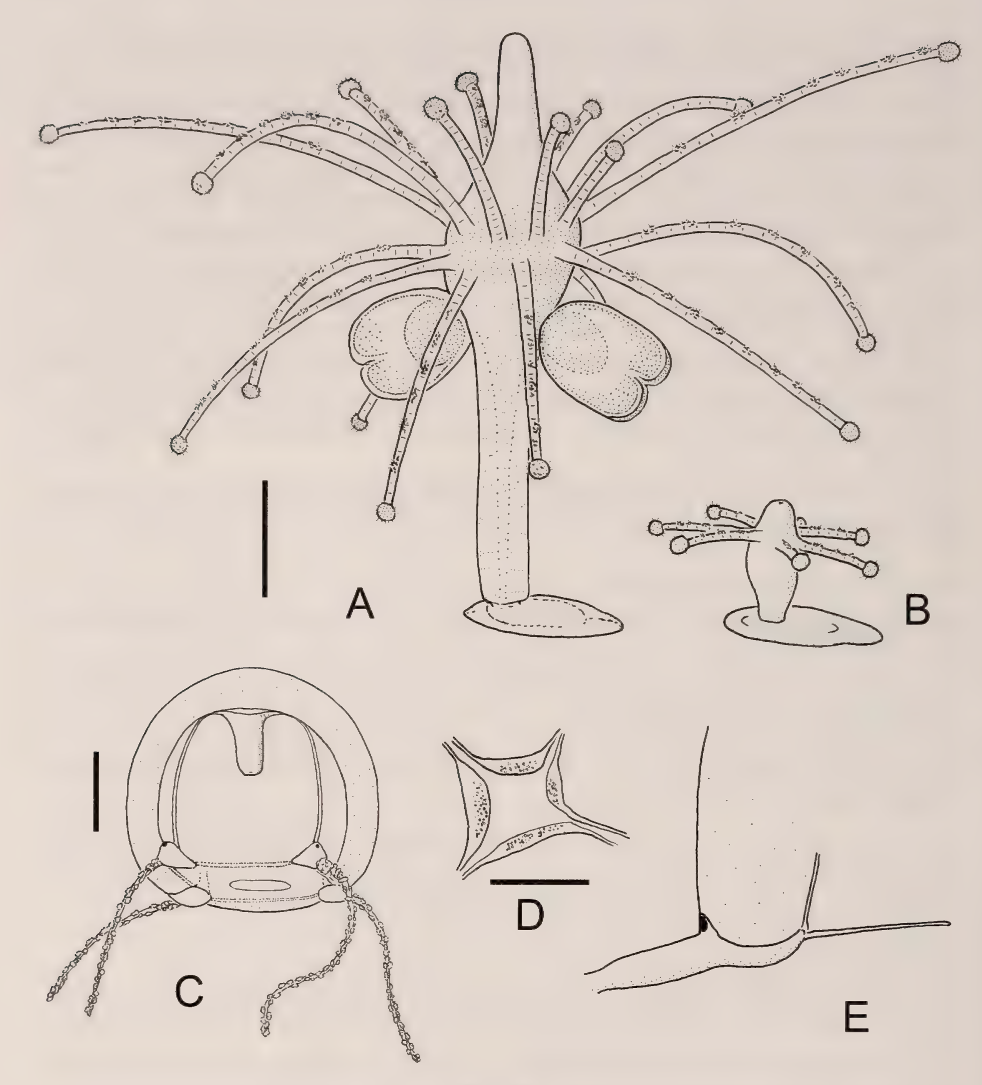


FIG. 59

Odessia maeotica (Ostroumoff, 1896); after life. (A) Fully grown polyp with medusa buds; scale bar 0.2 mm. (B) Young polyp, same scale as A. (C) One-day-old medusa; scale bar 0.2 mm. (D) Manubrium of newly liberated medusa in aboral view; scale bar 0.1 mm. (E) Vertical optical section of bell margin of a fully grown medusa showing marginal bulb with an abaxial ocellus and the tentacle base, at right the velum.

Odessia maeotica maeotica Picard, 1951: 6.
Odessia maeotica ostroumowi Picard, 1951: 6.
Odessia maeotica marina Picard, 1951: 9.
*Odessia maeotic*a forma *gallica*. – Picard, 1951: 11, figs. – Rees, 1958: 540, fig. 5.
in part *Moerisia maeotica*. – Naumov, 1969: 539, fig. 388.

MATERIAL EXAMINED: MHNG INVE 53642; France, Portiragnes Plage, mouth of small canal, 43.2689°N 03.36753°E, 07.04 2007, salinity 14 ppt, about 30 mature medusae, examined alive, polyps cultivated until new medusae released; DNA extracted from several individuals,

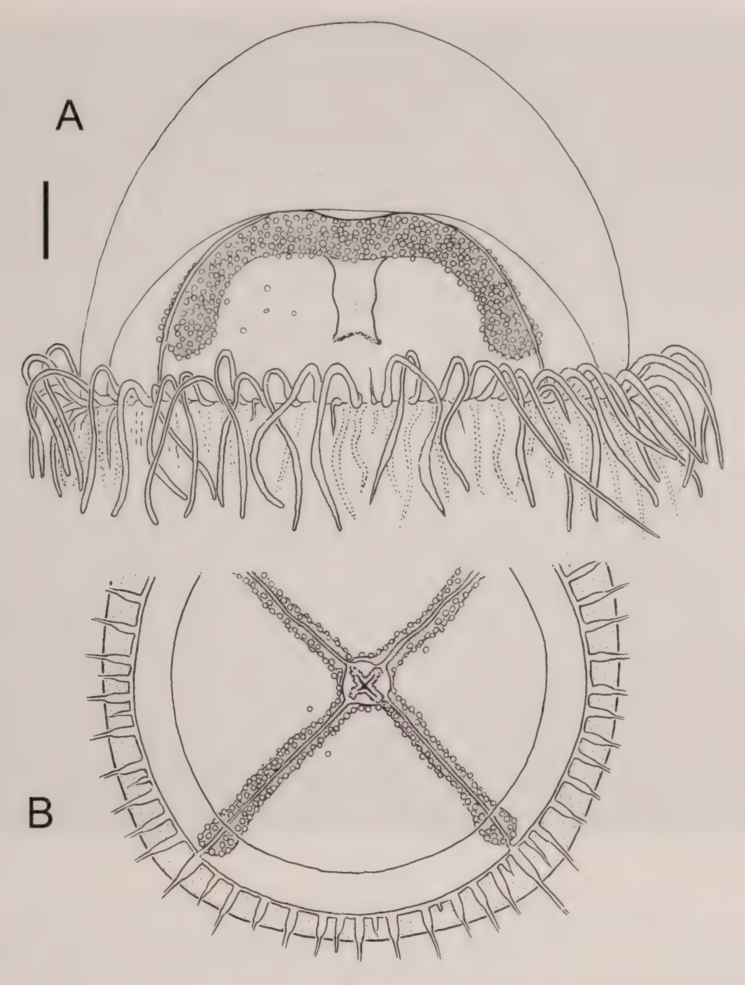


FIG. 60

Odessia maeotica (Ostroumoff, 1896); female medusa after life, scale bar 2 mm. (A) Lateral view. (B) Oral view.

sequences: 16S **GQ39532**, 18S **GQ424341**, 28S **GQ424314**. – MHNG INVE 53643; France, Portiragnes Plage, La grande Maire (brackish water lake), 09.04.2007, 2 medusae. – MHNG INVE 39463; France, Sigéan (brackish water lake); 21.07.1953. about 30 mature medusae.

DIAGNOSIS: Moerisiid medusa with 32 or more tentacles, nematocysts on tentacles in irregular buttons, not in rings. Gonads on long, perradial basal extension of manubrium. Polyps solitary, with solid, semimoniliform tentacles, medusa buds below tentacles.

DESCRIPTION: Polyps solitary, extended polyp subdivided into four regions: attachment disc, basal pedicel, hydranth body, and hypostome. Base of polyp ending in one attachment disc (podocyst) adhering to substrate, podocysts a shallow plano-convex perisarc capsule with small excentric opening. Pedicel of mature polyp

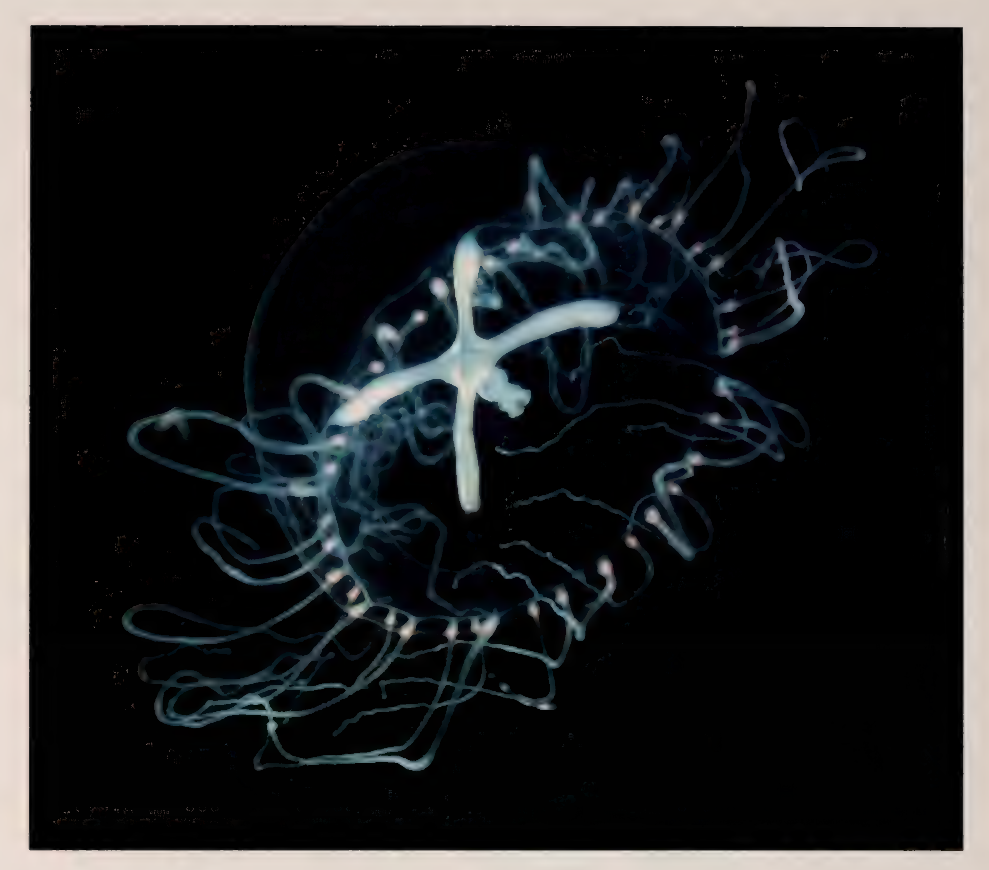


FIG. 61
Odessia maeotica (Ostroumoff, 1896); mature medusa.

comprises about ½ of total height, with large gastrodermal cells, lumen narrowed. Hydranth body about two times as thick as pedicel, rounded, bearing tentacles in middle region. Tentacles in two indistinct whorls or scattered, 16-20 in number, slender, contractile, expanded as long as polyp height, length variable (growth stages), with terminal nematocyst button, diameter about two time the stalk diameter, on stalk additionally irregular nematocyst patches on upper (oral) side (semimoniliform), gastrodermis chordoid. Hypostome elongated, proboscis-like, contractile, can be elongated to about the same length as hydranth body height, mouth region without concentration of nematocysts. Medusa buds below tentacles near junction to pedicel, 2-3 per hydranth, usually an opposite pair.

Colour: colourless or pigments from food items.

Nematocysts: stenoteles, desmonemes, microbasic heteronemes (mastigophores or euryteles with very faint swelling of shaft).

Newly liberated medusa with four tentacles, tentacular nematocyst clusters not in rings, with ocelli, manubrium tubular and short, exumbrella scattered with small heteronemes.

Adult medusa bell-shaped, nearly hemispherical or slightly wider than high, jelly very thick (1/3 to 1/2 of total height), subumbrella rather flat and with planar top. Manubrium composed of a central, tubular part and long perradial basal lobes. Central tube (stomach) cruciform in section, mouth four-lipped, margin densely beset with nematocyst clusters (stenoteles), sometimes slightly frilled. Perradial stomach lobes extending along ½ to ¾ of subumbrella radius, height only about 1/3 of total manubrium height. Gonads on perradial lobes of manubrium, not interrupted interradially in fully grown animals, bulging thick layer. The tubular part of the manubrium remains free of gonads. Females with numerous eggs that develop in situ into planula, hence larviparous. Four radial canals rather short as issued from stomach lobes, thin, ring canal thin. Tentacles 32-52, contracted shorter than bell, of variable size, tapering, base swollen, adnate and clasping bell margin, with short abaxial spur containing red ocellus, nematocysts concentrated into irregular clasping clusters, not in rings and thus not moniliform, distribution of capsules can change from clusters to evenly spread, gastrodermis hollow, often with brown pigment granules.

Colours: not coloured or only slightly so, brown pigment granules in tentacles.

Nematocysts: stenoteles, desmonemes, microbasic heteronemes (mastigophores or euryteles with very faint swelling of shaft); perhaps also some rare haplonemes present.

Dimensions: Medusa diameter when mature 9-16 mm, smaller sizes known (4 mm). Planula 0.2-0.3 mm. Polyp up to 1 mm high. Newly released medusa 0.65-0.72 mm high and 0.52-0.58 mm wide (Paspalew, 1936).

Nematocysts of polyp (living): stenoteles 9-10)x(6-8)μm; desmonemes (6-7)x(3-4)μm; microbasic heteronemes (7-8)x(2.5-3)μm, r=2.7-3.2. Nematocysts of medusa (living): larger stenoteles (10-11)x(7.5-8)μm; smaller stenoteles (7.5-8.5)x(6)μm; desmonemes (5.5-7)x(3-4)μm; microbasic heteronemes (7-8)x(2.5-3)μm, r=2.7-3.2.

Other data: In old polyps (after 3 months) up to 5 polyp buds can appear on the hydranth pedicel, thus leading to a small colony (Paspalew, 1936). Marfenin (1984) also studied these temporary colonies. The gonads may be interrupted interradially in younger specimens (Paspalew, 1936; Naumov, 1969).

Biology: The eggs develop into planulae. After release, the planula settles rapidly. It flattens and forms a perisarc cover. Within only one day a young polyp emerges. Medusa budding starts after the polyp has reached a size of about one 1 mm (after ca. 7 days, may depend on food availability). Detached hydroids are usually unable to re-attach. According to Paspalew (1936) it lives for about 90-120 days. It is able to live at temperatures of 0-26°C at salinities of 0.5-2.5%. The maturation of the medusa takes about 30-40 days. The medusa feeds mainly on copepods and their larvae. It is positively phototropic and negatively geotropic. The temperature at which it is active is 15-26°C, below 10° it becomes inactive. Bioluminescence was observed while the medusae were in their natural environment, but not in culture.

Distribution: Brackish water lagoons and lakes of the Mediterranean; Black Sea; Sea of Azov; Morocco (Atlantic side) (Ostroumoff, 1896; Mayer, 1910; Picard, 1951; Picard, 1955; Morri, 1981; Brinckmann-Voss, 1987). Two apparent records in

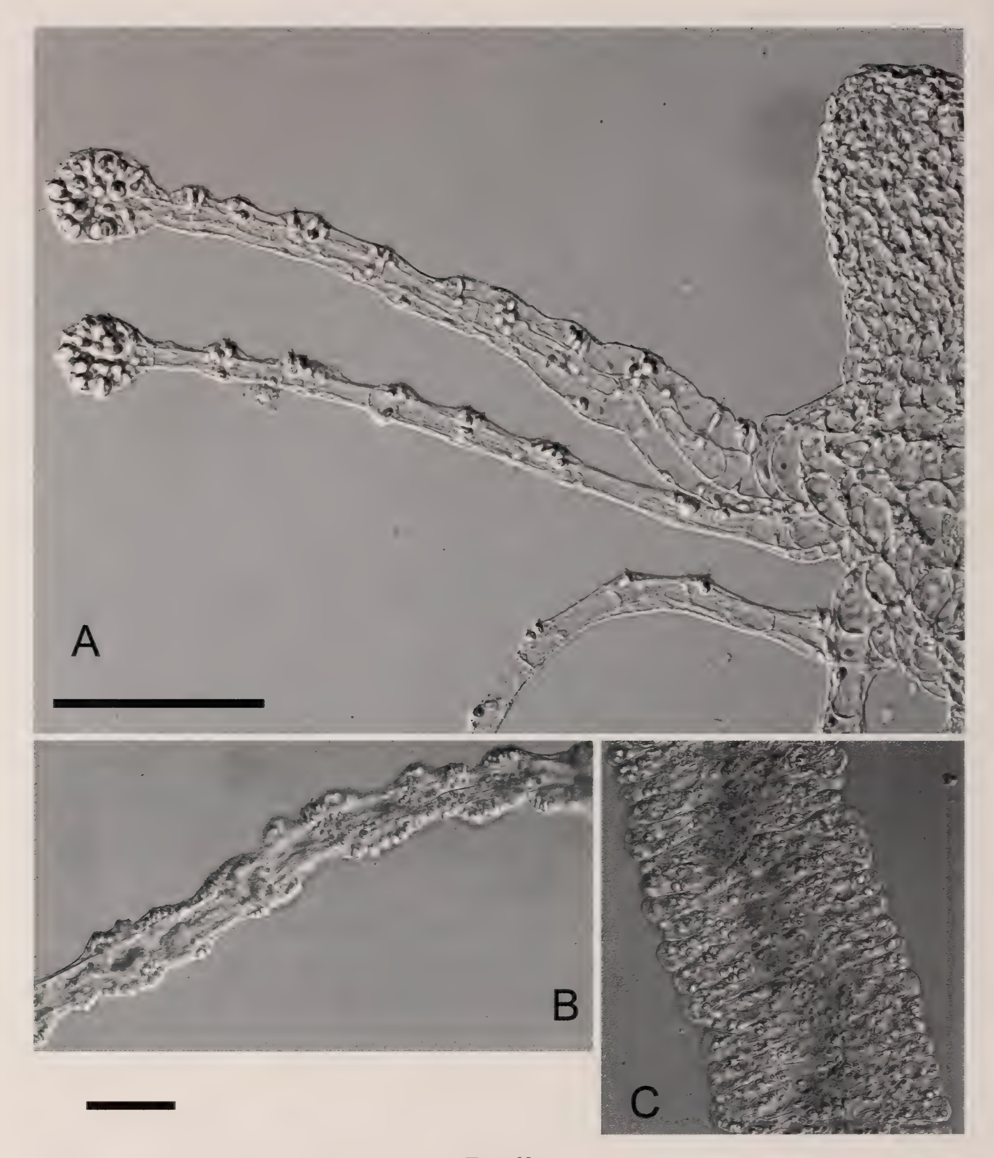


FIG. 62

Odessia maeotica (Ostroumoff, 1896); microphotographs of living animals. (A) Extended tentacles of polyp, note irregular nematocyst clusters on trunk of tentacle, scale bar 0.1 mm. (B) Part of extended tentacle of medusa; note the irregular nematocyst clustering; scale bar 0.1 mm. (C) Same as B, but contracted.

seawater of normal salinity (Mayer, 1910; Picard, 1951) are perhaps due to animals being swept into the sea from lagoons. Type locality: Sea of Azov.

REMARKS: Naumov (1969: 541) incorrectly synonymized *Moerisia inkermanica* Paltschikowa-Ostroumowa, 1925 with *Odessia maeotica*. Although the medusae are



FIG. 63

Odessia maeotica (Ostroumoff, 1896); cnidome, living capsules, scale bar 10 μm. (A-C) Medusa. (E-F) Polyp. (A) Stenoteles. (B) Desmonemes. (C) Microbasic heteronemes, top right discharged capsule. (D) Stenoteles. (E) Desmonemes. (F) Microbasic heteronemes.

very similar (distinguishable through the nematocyst arrangement of the tentacles), the polyps are rather different (comp. diagnoses).

According to Paspalew (1936), the gonads on the basal lobes may be separated from those of the central part. This could not be found in the material examined here and also Naumov (1969) regards it as a variable trait. Likewise, Paspalew (1936) stated that the newly released medusa has no exumbrellar nematocysts, which purportedly distinguishes it from *M. inkermanica*. In the sample examined here, the exumbrellae of young medusae were sprinkled with many very small nematocysts (heteronemes). They were only visible with the help of a compound microscope.

Picard (1951b) subdivided the species in four subspecies, mainly based on size differences.

Odessia maeotica maeotica: characterized by size of 18 mm diameter, up to 32 tentacles, distribution Sea of Azov.

Odessia maeotica ostoumowi: characterized by smaller size of 5-6 mm, Black Sea.

Odessia maeotica marina: characterized by size of 4-6 mm, 32 tentacles, occurs in fully marine conditions (may be misunderstanding), occurrence Casablanca, Naples, Trieste.

Odessia maeotica gallica: characterized by size of 5-8 mm, 32 or often more tentacles; larviparous; western Mediterranean.

Animals collected by myself in the region of Sète (type locality of *O. gallica* Hartlaub, 1917), however, had the same sizes as those of *O. maeotica* from the Sea of Azov. The subspecies *marina* is invalid as its distribution overlaps with *O. maeotica gallica*.

Family Sphaerocorynidae Prévot, 1959

Diagnosis: Hydroid colonial, stolonal or erect, hydrorhiza creeping; hydrocaulus long, unbranched or sparingly branched, with terminal hydranths; perisarc thin, reaching to hydranth base; hydranth pyriform with bulbous base and proboscis-like hypostome; no oral tentacles but numerous solid, single or trifid capitate tentacles in 3-5 whorls around broadest part of body; gonophores free medusae or sessile medusoids.

Free medusae with thick, dome-shaped or conical apical jelly, with large, broad apical chamber; four tentacles with adaxial, scattered, or spirally arranged nematocyst patches and hollow, ellipsoid terminal knob; tentacle bulbs large, clasping umbrella margin, provided with adaxial expansion; abaxial ocelli present; manubrium broadly flask-shaped, quadrate or cruciform in cross-section, narrowing to mouth tube with simple, more or less cruciform mouth; gonads adradial, confluent in perradii in mature specimens.

Remarks: The genus currently comprises three genera, *Sphaerocoryne* Pictet, 1893, *Corynetes* Haeckel, 1879, and *Heterocoryne* Wedler & Larson, 1986 (Bouillon *et al*., 2006; Calder, 2010). Only *Sphaerocoryne* occurs in the ERMS zone.

Genus ***Sphaerocoryne*** Pictet, 1893

Sphaerocoryne Pictet, 1893; type species *Sphaerocoryne bedoti* Pictet, 1893 by monotypy.

Diagnosis: Hydroid colony stolonal; hydrocaulus long, simple or slightly branched; hydranth vasiform, with numerous simple solid capitate tentacles in 3-5 close set whorls around broadest part; gonophores developing above or among tentacles, either directly on hydranth or on short blastostyles.

Medusae with thick dome-shaped or conical apical jelly, with large, broad apical chamber; four tentacles with adaxial, scattered, or spirally arranged nematocyst patches and hollow, ellipsoid terminal knob; tentacle bulbs large, clasping umbrella margin, provided with adaxial expansion; abaxial ocelli present; manubrium broadly

flask-shaped, quadrate or cruciform in cross-section, narrowing to mouth tube with simple, more or less cruciform mouth; gonads adradial, confluent in perradii in mature specimens.

REMARKS: See Calder (1988; 2010) and Petersen (1990) for the taxonomic history of the genus. *Linvillea* Mayer, 1910 has often been regarded as a junior synonym of *Sphaerocoryne* (e. g. Petersen, 1990; Bouillon *at al.*, 2006). However, Calder (2010) noted that *Linvillea* itself is a junior synonym of *Corynetes* Haeckel, 1879. If *Sphaerocoryne* and *Corynetes* are regarded conspecific, then *Corynetes* becomes the valid name, thus replacing the well established name *Sphaerocoryne*. In order to avoid this, Calder (2010) suggested retaining both *Sphaerocoryne* and *Corynetes* as distinct genera. This solution is recommendable until a molecular phylogeny clarifies the status and relationship of both names.

Sphaerocoryne bedoti Pictet, 1893 Fig. 64

Sphaerocoryne bedoti Pictet, 1893: 10, pl. 1 figs 5-6. – Mammen, 1963: 48, figs 16-18. – Millard & Bouillon, 1974: 13, fig. 1A. – Millard, 1975: 54, fig. 20E. – Wedler & Larson, 1986: 80, fig. 3C, a, b. – Calder, 1988: 61, figs 46-47. – Hirohito, 1988: 37, fig. 11d. – Petersen, 1990: 131, fig. 6C-D. – Calder *et al.*, 2003: 1179, fig. 4. – Bouillon *et al.* 2004: 84, fig. 47F-G. – Wirtz & Debelius, 2003: 19, fig'd. – Goy *et al.*, 1991: 103, fig. 6.

Clavatella multitentaculata Warren, 1908: 278, pl. 45 figs 7-9. – Mammen, 1963: 49, synonym. – Millard, 1975: 54, synonym.

Syncoryne flexiblis Fraser, 1938: 15, fig. 8.

Sphaerocoryne multitentaculata. – Yamada & Konno, 1973: 103, figs 1-2.

TYPE MATERIAL EXAMINED: MHNG INVE 27134; syntype colonies of *Sphaerocoryne bedoti* Pictet, 1893; collected 27.06-02.09.1890 in Bay of Ambon, Moluccas; two lots, both with pieces of sponges and several hydranths with medusae buds, moderately well preserved.

OTHER MATERIAL EXAMINED: MHNG INVE 60977; French West Indies, islands of Terre-de-Haut, Baie de Pompierre, 0-5 m; infertile polyps collected 23.03.2008; leg. & det. Horia Galea (material of Galea, 2008). – ZMUC, without registration number, Galapagos Islands, few infertile polyps collected 22.09.1967; leg. & det. J. Bouillon.

DIAGNOSIS: Hydroid as given in genus diagnosis, medusa buds above and among the tentacles, medusa without exumbrellar nematocyst rows, tentacular nematocyst buttons arranged spirally.

DESCRIPTION (own data; medusa after Yamada & Konno, 1973): Colonial hydroids with hydrorhiza and part of the stem usually embedded in sponge tissue. Hydrorhiza tubular, branched, covered by perisarc, giving rise to several hydranths on long pedicels. Pedicels unbranched, increasing slightly in diameter towards distal, covered by perisarc terminating just below hydranth, perisarc mostly smooth, some short annulated stretches may be present.

Hydranth pear-shaped, thick, with relatively long hypostome, in middle a narrow band of 15-40 tentacles (max. 70) in 3-4 indistinct, closely approximated whorls, sometimes a few tentacles grouped in indistinct vertical rows. Tentacles relatively long, capitate, length variable, nematocysts concentrated in distinct terminal nematocyst button.

Medusa buds develop initially above tentacles and sometimes among uppermost tentacles, with continued development of more buds they may replace the tentacles (reproductive exhaustion). Medusa buds singly or in groups of 3-6 on short blastostyles.

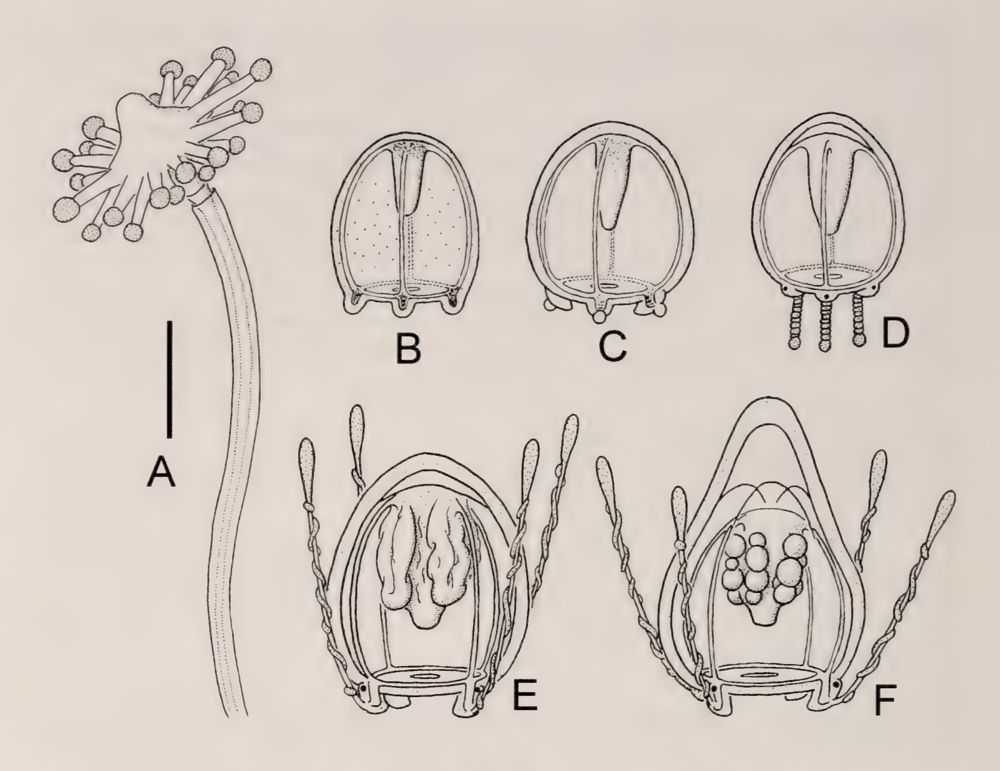


FIG. 64

? *Sphaerocoryne bedoti* Pictet, 1893. A after preserved material from the Galapagos Islands, B-F modified after Yamada & Konno (1973), originally drawn after living medusae from Japan; for sizes see text. (A) Hydroid, without medusa buds, scale bar 0.5 mm. (B) Newly liberated medusa. (C) 5-6 days old medusa. (D) More advanced medusa in swimming posture. (E) Fully mature male medusa in resting position. (F) Mature female with eggs, in resting position.

Nematocysts: stenoteles and desmonemes.

Newly liberated medusae nearly spherical, scattered nematocysts on exumbrella and not in meridional tracks, jelly thin, four radial canals, four small tentacle bulbs without ocelli, tubular manubrium spanning 1/3 to 2/3 of bell height, no oral structures, no incipient gonads, no tentacles. Four tentacles develop concurrently after release, all having about the same length at a time.

Mature medusae ovoid (male) to pear-shaped (females), without exumbrellar nematocyst rows, above manubrium a large apical chamber. Manubrium indistinctly cruciform in cross-section, without oral tentacles or other oral structures, in males two-thirds to four-fifths the height of the bell cavity, in females about two-thirds as long as bell cavity. Male gonads on perradial sectors of manubrium, composed of two vertical, adradial folds, protruding, relatively large and occupying a great part of the subumbrella. Female gonads with large eggs in adradial vertical rows. Four hollow marginal tentacles, relatively stiff and short, reaching lengths that slightly surpass the height of the bell, with a large, oblong terminal nematocyst cluster and 5-8 distinct nematocyst

clusters arranged nearly like a spiral on the whole length of the tentacle. Four radial canals ending in tentacle bulbs, each bearing a brown abaxial ocellus.

Nematocysts: stenoteles, desmonemes, and basitrichous haplonemes.

DIMENSIONS: Polyp stems 5-15 mm high, hydranth 0.5-1 mm, caulus diameter 0.11-0.15 mm. Newly liberated medusae 0.5-0.6 mm in diameter, adult male medusa male 2.5-3.0 mm in height and 2-3 mm in diameter, adult female 3-4.5 mm in height and 2-3 mm wide. For nematocyst measurements see Yamada & Konno (1973) and Calder (1988).

OTHER DATA: Preserved polyps of *Sphaerocoryne* usually have short and thick tentacles of somewhat variable length. The syntype specimens have some polyps with long and thin tentacles, although likely partly due to being squeezed during the collecting process. Wirtz & Debelius (2003) depict a living *Sphaerocoryne* polyp with long, thin tentacles radiating in all directions from the polyp body. It must thus be assumed that polyps in their natural environment extend the tentacles much more than shown in Fig. 64 (perhaps twice as long or more).

BIOLOGY: A relatively rare species, the polyp occurs almost exclusively partially embedded in sponges. Colonies are gonochoristic. Galea (2008) also found them on tubes of serpulid polychaetes. The medusa reaches maturity two weeks after liberation (Yamada & Konno, 1973).

DISTRIBUTION: Circumglobal in warm to temperate waters, known from Indonesia (Pictet, 1893), Japan (Yamada & Konno, 1973; Hirohito, 1988), Hawaii (Calder, 2010), Galapagos Islands (Calder *et al.*, 2003), Pacific coast of Colombia (Fraser, 1938 as *Syncoryne flexiblis*), India (Mammen, 1963), East Africa (Millard & Bouillon, 1974), South Africa (Warren, 1908; Millard, 1975), Bermuda (Calder, 1988), Puerto Rico (Wedler & Larson, 1986). In the ERMS zone recorded as polyp phase from the island of Madeira (Wirtz & Debelius, 2003) and in the eastern Mediterranean in its medusa phase (Goy *et al.*, 1991; one infertile medusa). Type locality: Bay of Ambon, Moluccas.

REMARKS: The nominal species *S. bedoti* is based on polyp colonies bearing medusa buds that were originally found in the Moluccas (Pictet, 1893). The medusa has never been reared from polyps of the same geographic region. There is only one *Sphaerocoryne* medusa known from the region, namely *S. peterseni* Bouillon, 1984a, characterized by adaxial tentacular nematocyst buttons. The polyp stage of *S. peterseni* is not known with certainty, although Bouillon (1984a) found numerous *Sphaerocoryne* polyps at the type locality of *S. peterseni*, but he was unable to link it them reliably to the mature medusa from the plankton. It seems nevertheless possible that *S. peterseni* could be the medusa stage belonging to *S. bedoti* and perhaps not the medusa described by Yamada & Konno (1973). These authors found a *Sphaerocoryne* polyp in northern Japan which they identified as *S. multitentaculata*, a species originally described from South Africa. Mammen (1963) and Millard (1975) synonymized *S. multitentaculata* with *S. bedoti*, a conclusion which was adopted by subsequent authors (e. g. Calder, 1988; Petersen, 1990; Bouillon *et al.*, 2006). Yamada & Konno reared the medusae originating from this hydroid to maturity and it was taken as representing *S. bedoti* by subsequent authors (e. g. Millard, 1975; Petersen, 1990).

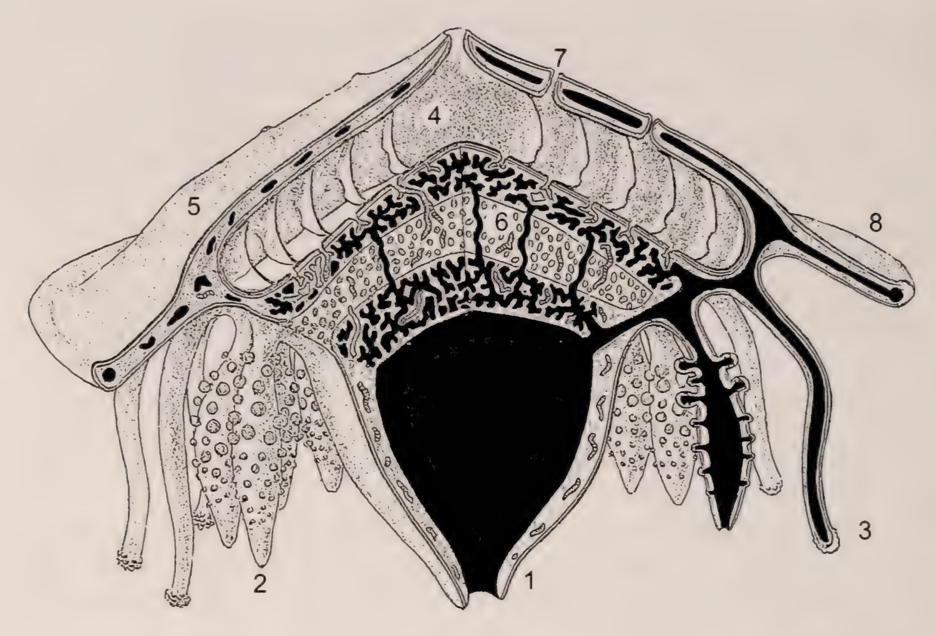


FIG. 65

Schema of a hypothetical Porpitidae showing the principal elements of the hydroid phase, in black common gastrocoel. Modified after Delage & Hérouard (1901). (1) Gastrozooid. (2) Gonozooid. (3) Dactylozooid. (4) Pneumatophore or float with air-chambers. (5) Mantle. (6) Central organ, upper layer called "liver", middle layer with nematoblasts, and lower layer ("kidney"). (7) Pores (stigmata) leading into air-chambers. (8) Limbus or part of mantle not supported by chondrophore.

Although this may be correct, new rearing experiments using material from the type locality have to confirm the identity of the medusa of *S. bedoti*.

Several authors identified *Sphaerocoryne* polyps without medusa buds as *S. bedoti*. This is not recommendable as there are no reliable diagnostic differences that would allow distinguishing polyps of *S. bedoti* and *C. agassizii* (McCrady, 1859) (comp. Yamada & Konno, 1973). Both species differ in their medusa phase. *Corynetes agassizii* has eight rows of exumbrellar nematocysts, its tentacular nematocyst buttons are small and scattered and not long and spirally arranged, and the young medusae have two opposite tentacles only (Mayer, 1910; Calder, 1971; Yamada & Konno, 1973). The polyps differ according to Yamada & Konno (1973) in the position of the medusa buds: among the tentacles in *C. agassizii*, above the tentacles in *S. bedoti* (resp. *S. multitentaculata*). A re-examination of the type material of *S. bedoti* showed that the medusa buds are not only developing above the tentacles, but also among the distalmost tentacles. When there are many buds, they can even replace the tentacles. Such a tentacle reduction has also been mentioned by Pictet (1893) and is also known for many other hydroids and termed reproductive exhaustion.

The records of *S. bedoti* for the ERMS zone are based on infertile polyps from Madeira and on a single, infertile medusa from Lebanon. More data are needed to reliably ascertain the presence of this species the ERMS zone.

Family Porpitidae Goldfuss, 1818

Porpitae Goldfuss, 1818, emended to Porpitidae by Guilding (1828).
Velellidae Eschscholtz, 1829.
Discalidae Haeckel, 1888a.
Porpalidae Haeckel, 1888b.
Porpitellidae Haeckel, 1888b.

Diagnosis: Hydroid a floating colony with polymorphic polyps on underside, with a large central gastrozooid surrounded by gonozooids and peripheral dactylozooids. Float contains a perisarc disc with concentric air chambers and a complex system of gastrodermal canals. Gonophores develop on gonozooids and are liberated as medusae.

Umbrella of medusa with four or eight tracks of nematocysts originating from marginal bulbs. Four or eight radial canals ending in marginal bulbs, ring canal present. Manubrium short, with circular mouth. Gonads perradial or interradial, may be irregularly developed so that number may vary. Two opposite marginal tentacles ending in spherical nematocyst knob, with or without two additional smaller capitate tentacles on adaxial side of bulbs bearing long tentacles. No ocelli. Zooxanthellae often present.

Remarks: For the taxonomic history of the Porpitidae see Brinckmann-Voss (1970) and Calder (1988). Following Totton (1954), Petersen (1990) and Bouillon *et al*. (2006), the family is here seen as comprising only the two genera *Porpita* and *Velella*. The family has a long geologic history (see e. g. Fryer & Stanley 2004; Waggoner & Collins, 2004).

Key to the genera

1a	polyp stage	2
1b	mature planktonic medusa	3
2a	round, floating colony without sail	*Porpita*
2b	oval floating colony; with a median sail	*Velella*
3a	8 radial canals, 2 opposite capitate tentacles	*Porpita*
3b	4 radial canals; 2 opposite pairs of capitate tentacles	*Velella*

Genus ***Porpita*** Lamarck, 1801

Porpita Lamarck, 1801; type species *Medusa porpita* Linnaeus, 1758 by absolute tautonomy.
Polybranchionia Guilding, 1828; type species *Polybranchonia Linnaeana* Guilding, 1828 by monotypy.
Ratis Lesson, 1830; type species *Ratis Medusae* Lesson, 1930 by monotypy.
Acies Lesson, 1830; type species *Acies Palpebrans* Lesson, 1930 by monotypy.
Chrysomitra Gegenbaur, 1857; type species *Chrysomitra striata* Gegenbaur, 1857 by monotypy.
Discalia Haeckel, 1888a; no type species specified.
Disconalia Haeckel, 1888a; no type species specified.
Porpitella Haeckel, 1888a; invalid junior homonym of *Porpitella* Pomel, 1883. [Echinodermata]
Porpalia Haeckel, 1888a; type species *Porpalia prunella* Haeckel, 1888b, by designation of Haeckel (1888b).
Porpema Haeckel, 1888a; type species *Porpema lenticula* Haeckel, 1888a by designation of Haeckel (1888b), but this is apparently a *nomen nudum*.
Discomitra Haeckel, 1888b; medusa of *Disconalia gastroblasta* Haeckel, 1888b.

Diagnosis: Porpitid hydroids with circular-shaped float and mantle. Float either flat or convex, with or without central bulge, without sail. Dactylozooids with three vertical rows of short, capitate tentacles.

Medusa with small manubrium; juveniles without tentacles, four radial canals; adults with two capitate tentacles and normally eight radial canals, their gastrodermal cells containing algal symbionts.

REMARKS: The synonymy given above was taken from Calder (1988), only *Discalia*, *Porpalia*, and *Porpema* were added (see Bigelow, 1911 and Totton, 1954). The systematics of this genus remains unsatisfactory and a new, comprehensive study using molecular markers is needed. Totton (1954) thinks that there are only two valid species, *P. porpita* and *P. prunella* (Haeckel, 1888b), but their status is not well resolved. Only *P. porpita* is present in the ERMS zone.

Porpita porpita (Linnaeus, 1758) Figs 66-67

SYNONYMY: The synonymy of this species is very long, comprising more than 30 nominal species and even more combinations. Calder (1988) and Bigelow (1911) should be consulted for a comprehensive list.

CONSULTED WORKS:
Medusa porpita Linnaeus, 1758: 659.
Porpita mediterranea. – Kölliker, 1853: 57, pl. 12.
Chrysomitra striata Gegenbaur, 1857: 232, pl. 7 figs 10-15. – Bouillon, 1984b: 254.
Porpita Linnaeana. – Agassiz, 1883: 12, pls 7-12.
Porpita umbella. – Chun, 1897: 90.
Porpita porpita. – Bigelow, 1911: 353. – Delsman, 1923: 243, figs 1-28. – Prévot, 1959: 106, pl. 5 fig. 17. – Brinckmann-Voss, 1970: 38, figs 40-42. – Daniel, 1979: 111, fig. 1a-d. – Bouillon, 1984b: 249, figs 1-2. – Calder, 1988: 77, figs 65-57. – Pagès *et al*., 1992: 23, fig. 22. – Schuchert, 1996: 98, fig. 58a-b.
Porpita pacifica. – Bigelow, 1911: 333, pl. 28, fig. 1-10, 12, 13, 14, pl. 29.

MATERIAL EXAMINED: MHNG INVE 54652; Italy, Naples; 2 colonies collected before 1882, diameter 12-15 mm, with medusa buds. – BMNH 1984.3.23.1; Papua New Guinea, Hansa Bay, Laing Harbour; about 20 colonies collected by J. Bouillon in August 1978, very well preserved.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION (Delage & Hérouard, 1901; Brinckmann-Voss, 1970; Bouillon, 1984; Calder 1988; own data): Hydroid colony relatively large, floating on water surface, with disc-shaped mantle, internal float, and polyps on underside. Upperside slightly convex, usually without tubercles, central region sometimes with round elevation (umbo), with a small central pore and numerous small pores (stigmata) in radiating rows. Mantle diameter larger than internal float and with free, soft margin (limbus), beneath surface of mantle radiating gastrodermal canals. Central region firm due to internal chitinous float (pneumatophore) consisting of a series of concentric air-chambers with pores on upper side.

Between underside of float and central gastrozooid lies the disk-shaped central organ, composed of a complicated system of canals in a mass of nematoblasts. Canals of two types, gastrodermal canals continuous with the gastric cavity of the gastrozooid and air-canals ("tracheids") connected to the pneumatophore. Central organ subdivided into three horizontal layers, an upper layer ("liver") with a dense concentration of canals with dark pigments and zooxanthellae, a median layer with fewer canals but more nematoblasts, and a basal layer again with numerous canals accompanied by a white precipitate of crystalline guanine ("kidney").

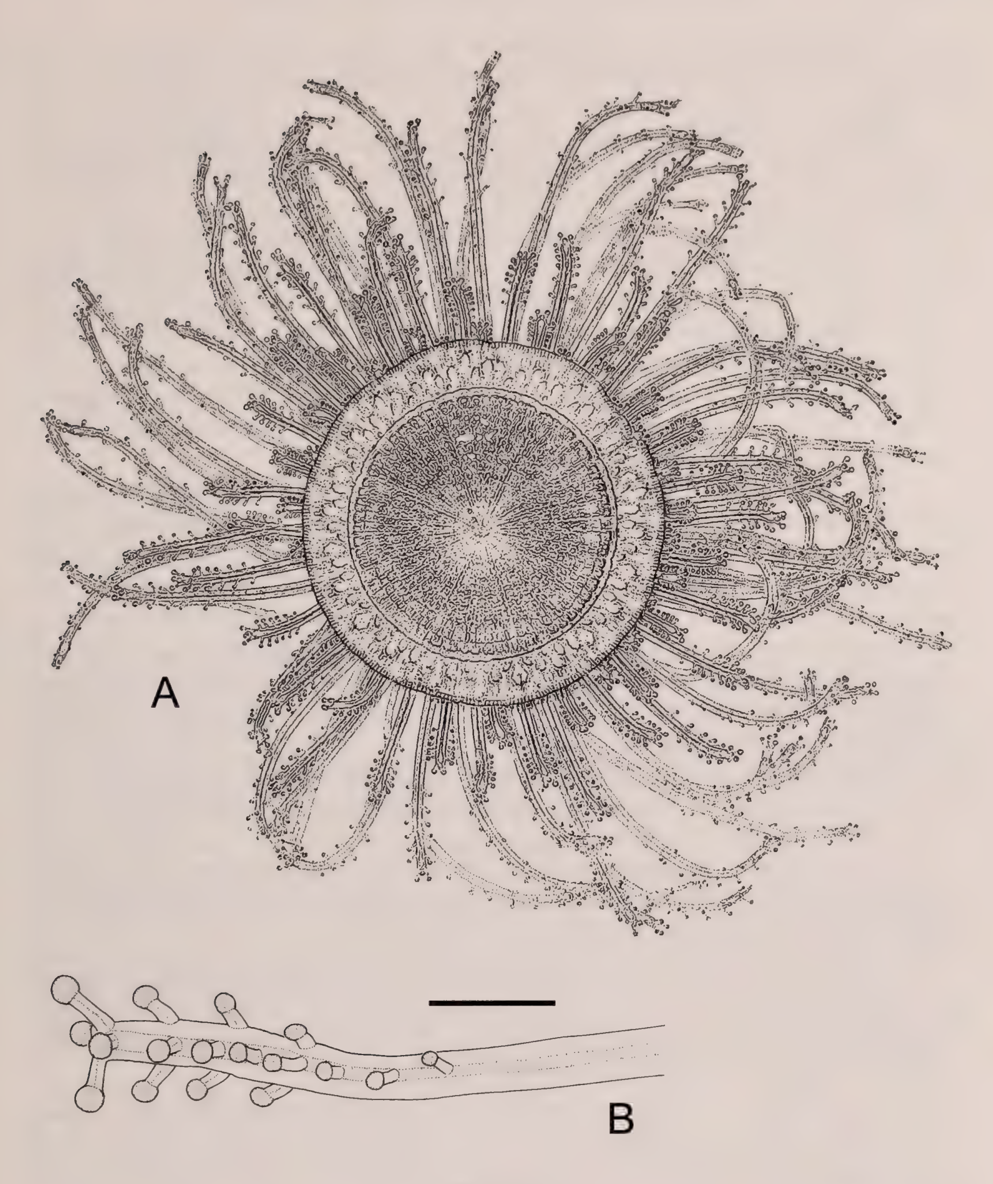


FIG. 66

Porpita porpita (Linnaeus, 1758). (A) Hydroid colony seen from above, size about 2.5 cm, drawn and modified after photograph of living animal from the western Atlantic (source: oceanexplorer.noaa.gov). (B) Dactylozooid, after preserved material from Naples, scale bar 1 mm.

Undersurface of colony with one large central gastrozooid, a median band of numerous gonozooids, and a peripheral band of dactylozooids.

Central gastrozooid circular, short and broad with a terminal mouth, without tentacles or prominent nematocyst clusters.

Gonozooids clavate, lacking tentacles but instead with wart-like nematocyst-clusters, four around mouth and more scattered over body, medusae develop near base in clusters.

Dactylozooids with tentacles, with a distal whorl of four capitate tentacles, body with varying number (14-20) of capitate tentacles in three longitudinal rows; mouth absent.

Nematocysts: three types of stenoteles, atrichous isorhizas, haplonemes.

Colours: Mantle and dactylozooids usually intensely blue, centre of float region silvery due to the enclosed gas or underlying tissue shining through yellow to brown.

Young medusa bell-shaped, slightly higher than wide. On exumbrella four rows of stenotele capsules. Manubrium very short. With four broad, radial gastrodermal strands, circular canal missing. Tentacles lacking. Gastrodermal system without lumen, composed of large, vacuolated cells. Gastrodermis of radial canals with zooxanthellae. Unable to feed during first five days after its liberation.

Adult medusa bell rather conical, with jelly of even thickness. Exumbrella with eight perradial tracks of nematocysts, only one capsule wide. Manubrium length 1/3 of bell cavity, conical, with circular, hardly visible mouth. Gonads normally in four perradial masses on manubrium, but three to eight gonads may be present. Only two tentacles present, usually opposite, but sometimes not. Tentacles long, thin, ending in a voluminous terminal swelling. Tentacles develop unequally and are often of different length, often only one tentacle present. Eight broad radial canals with zooxanthellae, exceptionally other numbers ranging from 10 to 16, circular canal present, eight little developed marginal bulbs without ocelli.

Nematocysts: stenoteles and telotrichous macrobasic euryteles, shaft length about 7 times the capsule length, present only relatively late in development.

Young hydroid colony drifting in plankton and not on water surface, with swollen, subspherical central gastrozooid, near its aboral side a ring of incipient gonozooids, a ring of dactylozooids with capitate tentacles, and a small disc-shaped float and mantle (for more details see Delsman, 1923).

Dimensions: Floating hydroid colony up to 3 cm in diameter, more usually 1-2 cm, sometimes up to 5 cm. Planktonic colonies up to 3 mm. Young medusa 0.3 mm. Adult medusa up to 2.5 mm high and 2 mm in diameter (Bouillon, 1984b). For nematocyst sizes see Calder (1988) and Bouillon (1984b).

Distribution: Hydroid circumglobal in tropical to warm-temperate waters (Moser, 1925; Brinckmann-Voss, 1970). In the ERMS zone, it is apparently confined to the Mediterranean and to the region south of the Strait of Gibraltar (Chun, 1897; Brinckmann-Voss, 1970; Wirtz & Debelius, 2003). Type locality: India (Linnaeus, 1758). The mature medusa has only been seen in the tropical western Pacific (Bouillon, 1984b) and perhaps also the Mediterranean (Gegenbaur, 1857).

Remarks: *Porpita* is a rather complex organism and a detailed description of its morphology would be suitable for a monograph of its own. More details than given here and also other pertinent information and more references, can be found in e. g. Agassiz (1883), Bigelow (1911), Hyman (1940), Totton (1954), Brinckmann-Voss (1970), and Calder (1988). The development of the medusa buds and also of the young colony was described in detail by Delsman (1923).

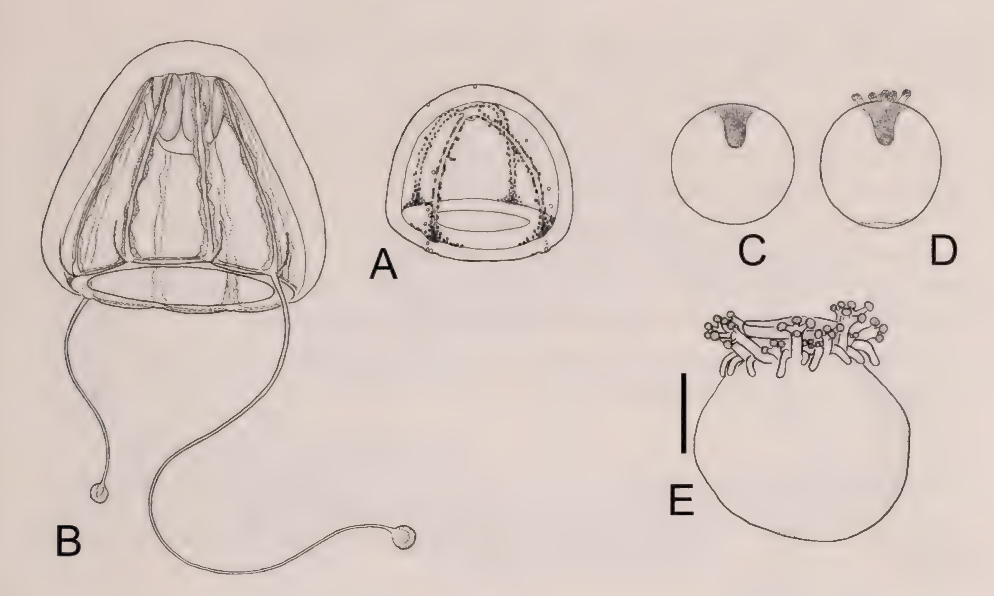


FIG. 67

Porpita porpita (Linnaeus, 1758). (A) Newly liberated medusa, from Delsman (1923). (B) Mature medusa from Papua New Guinea, height 2 mm, redrawn and modified after Bouillon (1984b). (C) Earliest known developmental stage of the hydroid colony, a hollow sphere (future gastrozooid) with an inward-projecting cone of cells (anlagen of gastrodermal canals, nematoblast disk, and pneumatophore); orientation as in mature colony; from Delsman (1923). (D) More advanced larval stage with beginning formation of the tentacles, from Delsman (1923). (E) Young colony, scale bar 1 mm, modified after Calder (1988).

Gegenbaur (1857) described under the name *Chrysomitra striata* a medusa he had collected near Messina in the Mediterranean. Due to the similarities with newly liberated medusae of *Velella velella* he assumed that it could be the adult medusae of this species. Gegenbaur had three mature animals measuring about 6.5 mm in height and width, they all had 16 broad radial canals, 16 meridional lines of nematocysts on the exumbrella, four gonads on a small manubrium, and "yellow cells" along the radial canals. One of the medusae had a single tentacle with a spherical nematocyst cluster at its end. This medusa obviously resembles the medusa of *P. porpita* described by Bouillon (1984b) and Bouillon thought it to be conspecific, despite the twofold higher number of radial canals. If not only due to different sizes and ages, this difference could also indicate that Bouillon's population from the Pacific and Gegenbaur's Mediterranean animals belong to distinct species or subspecies.

Genus ***Velella*** Lamarck, 1801

Velella Columnae, 1616. [not binomial]
Armenistari Carburi, 1757. [not binomial]
Phyllodoce Browne, 1789. [invalid name, published in a suppressed work, ICZN Opinion 89]
Velella Lamarck, 1801; type species *Medusa velella* Linnaeus, 1758 by absolute tautonomy.
Rataria Eschscholtz, 1829; no type species designated.
Armenistarius Costa, 1835; emendation of *Armenistari* Carburi, 1757.

Armenistarium Costa, 1841, emendation of *Armenistarius* Costa, 1835.
Velaria Haeckel, 1888a; preoccupied for Porifera.
Armenista Haeckel, 1888a; no type species designated.

DIAGNOSIS: Floating porpitid hydroid colonies with an oval float and mantle, bearing an upright sail set diagonal to long axis of float; on underside single central gastrozooid, feeding gonozooids and dactylozooids.

Free medusa with radial exumbrellar nematocyst rows, four radial canals and four perradial marginal bulbs, two opposite bulbs each with one long abaxial and one short adaxial capitate tentacle, other two marginal bulbs without tentacles. Stomach with tubular mouth. Gonads in male divided. Female with one egg.

REMARKS: The synonymy given above was largely taken from Calder (1988). The genus is currently monotypic.

Velella velella (Linnaeus, 1758) Figs 68-69

SYNONYMY: The synonymy of this species is extraordinarily long (>30 names). Vogt (1854), Bigelow (1911), Arai & Brinckmann-Voss (1980), and Calder (1988) should be consulted for synonyms, name combinations, and detailed lists.

CONSULTED WORKS:
Urtica marina soluta rarior, *Velella*, dicta. – Columnae, 1616: XX, pl. 22.
Medusa velella Linnaeus, 1758: 660.
Velellameduse. – Metschnikoff, 1886b: 1, pl 1 figs 1-5.
Velella. – Huxley, 1858: 107, pl. 11. – Woltereck, 1904: 351, figs A-B, pls 17-19.
Velella spirans. – Vogt, 1854: 5, pls 1-2. – Kölliker, 1853: 57, pl. 11 figs 9-15. – Chun, 1897: 93, fig. 2. – Vanhöffen, 1906: 37, figs 58-63. – Leloup, 1929: 402, figs 1-6, pl. 10-12.
Velella mutica. – Agassiz, 1883: 2, pls 1-6.
Velella lata. – Bigelow, 1911: 343.
Velella velella. – Bigelow, 1911: 353. – Russell, 1939: 358. – Totton, 1954: 34. – Prévot, 1959: 109, pl. 4 fig. 20. – Brinckmann, 1964: 327, figs 1-3. – Edwards, 1966: 283. – Brinckmann-Voss, 1970: 34, figs 36-39. – Bouillon, 1978a: 148. – Daniel, 1979: 118, fig. 1m-n. – Arai & Brinckmann-Voss, 1980: 14, fig. 6-7. – Larson, 1980: 183, fig. 1. – Kirkpatrick & Pugh, 1984: 143, fig. 61A-E. – Calder, 1988: 81, figs 58-59. – Pagès *et al*., 1992: 21, fig. 21. – Schuchert, 1996: 99, fig. 59a-f.

MATERIAL EXAMINED: MHNG INVE 26688; USA, California, collected June 1999; 4 specimens, all L-form, up to 4 cm long, length-width ratio of float 1.8. – MHNG INVE 54641 through 54648; Mediterranean, France; numerous specimens in 8 different lots, collected before 1895; in all lots >90% L-forms, shape of float always very elongate, length-width ratio of float 2.3-3.1. – MHNG INVE 54649; Mediterranean, France; > 20 specimens collected 1855 by C. Vogt, all L-form, length-width ratio of float 2.2-2.4. – MHNG INVE 54650; Mediterranean, Italy, Naples; 3 specimen collected before 1882, all L-form, length-width ratio of float 2.4. – MHNG INVE 54651; Mediterranean, France, Villefranche-sur-Mer; > 30 Rataria stages and young colonies up to 1 mm. – Mediterranean, Villefranche-sur-Mer, Ligurian Sea; 03.05.2001; millions of animals beached, observed polyp and medusa stage alive, none preserved, 16S **EU305487**.

DIAGNOSIS: As for genus.

DESCRIPTION (Woltereck, 1904; Brinckmann-Voss, 1970; Larson, 1980; Calder 1988; own data): Hydroid colony relatively large, floating on water surface, with flattened oval float, an upright, triangular sail, and polyps on underside. The long axis of the sail is oblique to the long axis of the float, being shifted either to the right or left of that axis, thereby creating two mirror-symmetric forms (Fig. 68F-G).

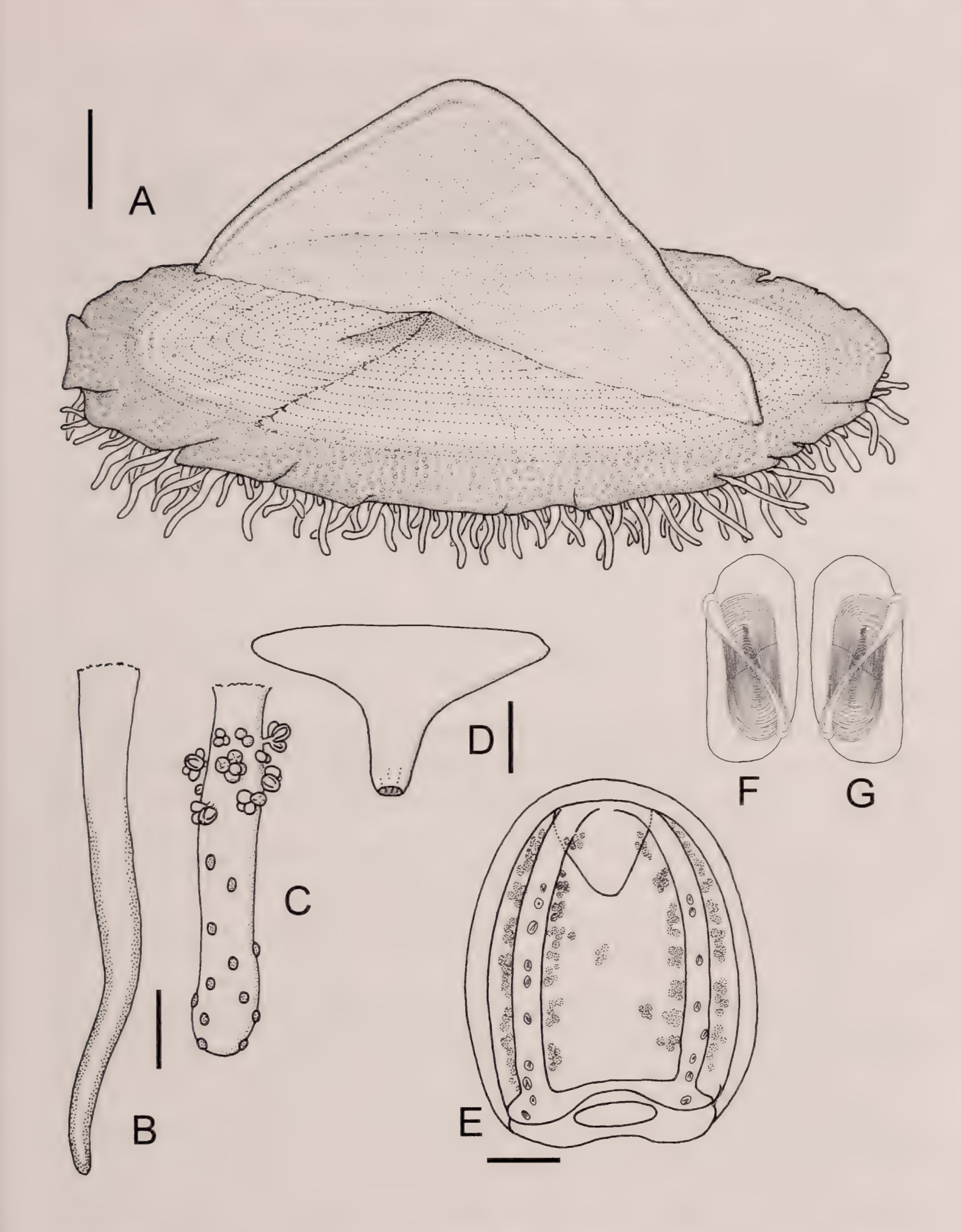


Fig. 68

Velella velella (Linnaeus, 1758); A-E, after animals from New Zealand, modified from Schuchert (1996). (A) Oblique lateral view of hydroid colony, scale bar 0.5 cm. (B) Dactylozooid, scale bar 1 mm. (C) Gonozooid, same scale as B. (D) Gastrozooid, scale bar 2 mm. (E) Newly liberated medusa, zooxanthellae stippled dark, scale bar 0.2 mm. (F) Top view of L-form colony (left-sailing, sail running from NW-SE). (G) Top view of R-form colony (right-sailing, sail running from NE-SW).

Upper side of float exposed to air, oval to rectangular shape, slightly conical in profile, tissue covering (= mantle) velvety, with gastrodermal canals and symbiotic algae, especially towards float margin. Small pores (stigmata) usually present in low numbers along base of sail, 2-4 on each side in the larger half of the float. Mantle larger than internal rigid support and with free, soft margin (= limbus), limbus in European populations relatively broad (ca. ¼ of shorter diameter). Central region firm due to internal chitinous float (= pneumatophore). Pneumatophore transparent, chitinous, consisting of a series of concentric air chambers forming a shallow cone, on this base sits the triangular support of the sail, support of sail without air chambers. Outline of pneumatophore oval, rectangular, or even slightly S-shaped. In European population the length to width ratio is 2.1-3.1, sail about as high as the shorter diameter of the pneumatophore. A diagonal fault line runs across the pneumatophore in mirror symmetry to the sail base.

Between underside of float and central gastrozooid is the disk-shaped central organ, composed of a complicated system of canals in a mass of nematoblasts ("liver"). Canals of two types, gastrodermal canals continuous with the gastric cavity of the gastrozooid and air-canals ("tracheids") connected to the pneumatophore. White precipitate of crystalline guanine absent.

In centre of underside a single, large gastrozooid encircled by a band of medusae producing gonozooids and a peripheral band of dactylozooids.

Central feeding zooid broadly oval with an elongated hypostome, without tentacles or medusae buds.

Gonozooids spindle-shaped with a swollen mouth region, lacking tentacles but with warts of nematocyst clusters concentrated in distal half. On proximal half of hydranth numerous medusae buds growing in groups from short blastostyles. Mouth present, zooids able to feed.

Dactylozooids long and tapering, oval in cross section with nematocysts concentrated on the narrow sides, mouth lacking.

Nematocysts: stenoteles, microbasic euryteles, isorhizas.

Colours: float deeply blue when alive, medusae buds yellow-olive due to symbiotic algae.

Newly released medusa bell-shaped, manubrium short, conical, red colour often present, unable to feed for the first few days. With four perradial rows of stenoteles on exumbrella originating from the marginal bulbs. With four broad radial canals ending in four broad marginal bulbs connected by radial. With or without two incipient opposite tentacles. Zooxanthellae in groups along the radial and circular canals. Nematocysts: stenoteles, macrobasic euryteles.

Adult medusa bell-shaped to cylindrical with flat top, jelly evenly thin. Manubrium conical, length 1/2 to 2/3 of bell cavity. Gonads on manubrium, in males as longitudinal swellings, position and number variable, 3-4 perradial gonads plus sometimes 2-3 additional interradial ones; female with one large, red egg. With four marginal bulbs. Two opposite bulbs lack tentacles, and the other bulbs have two capitate tentacles each, a short stout adaxial tentacle and a long abaxially-directed tentacle. Tentacles with parenchymatic gastrodermis. On the abaxial side of each tentaculate marginal bulb is a triangular patch of about 50 stenoteles which extends in

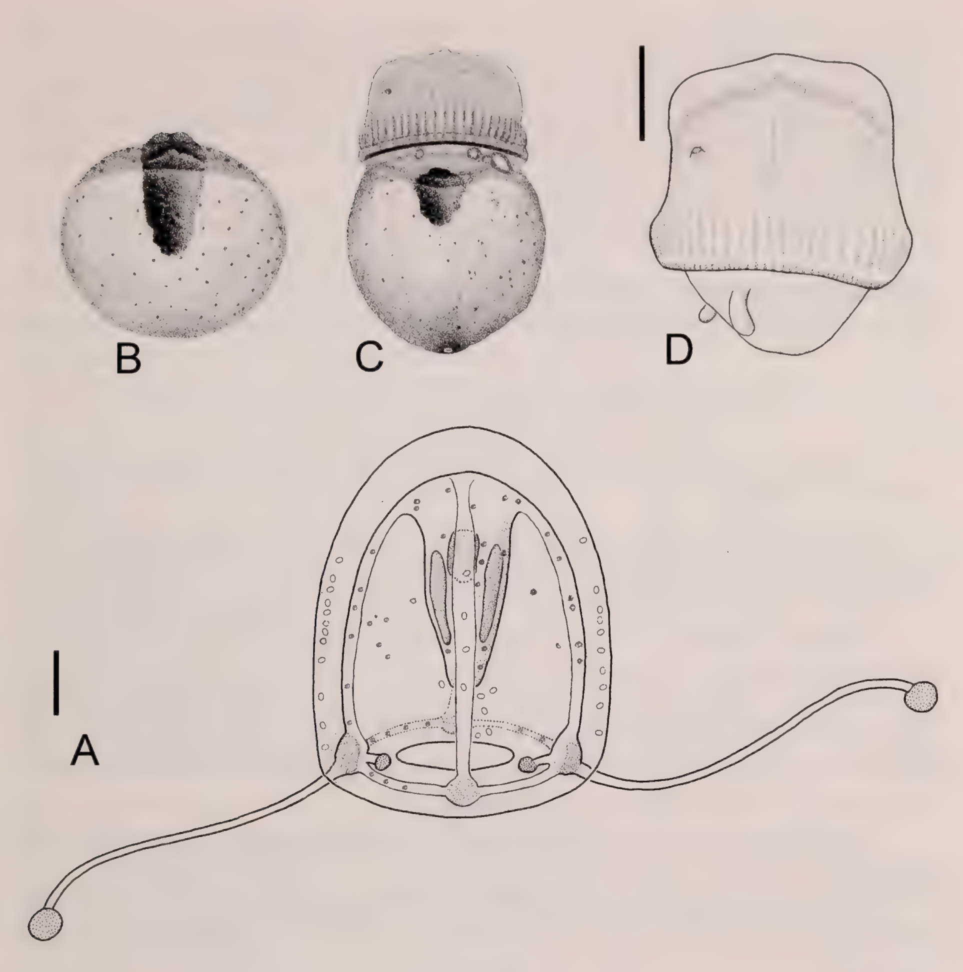


Fig. 69

Velella velella (Linnaeus, 1758). (A) Mature, cultivated medusa, scale bar 0.2 mm; redrawn modified after Brinckmann-Voss (1970). (B) Conaria larva, earliest known developmental stage of the hydroid, a hollow sphere (the future gastrozooid) with an inward-projecting, deep-red cone of cells (anlagen of gastrodermal canals and pneumatophore), same orientation as adult, size about 1 mm, from Woltereck (1904). (C) Somewhat later stage than in B, beginning formation of the pneumatophore, note mouth opening on underside; from Woltereck (1904). (D) Stage following C, Rataria larva, with beginning tentacle formation, the small cone in the upper left is a pore (stigma); scale bar 0.5 mm; after preserved material from the Mediterranean.

an irregular line to the bell apex. On the abaxial side of each atentaculate bulb 15 to 20 stenoteles forming a vertical, irregular double row extending a short distance from the bell margin, and continuing as an irregular line to the bell apex. Marginal sense organs absent.

Nematocysts: stenoteles, macrobasic euryteles.

Colour: umbrella dark brown due to zooxanthellae.

The development of polyp colony takes place in deep water. The youngest known stage (conaria larva) is a hollow sphere representing the future gastrozooid with an inward-projecting, deep-red cone of cells (anlagen of gastrodermal canals and pneumatophore) (Fig. 69B). Later developmental stages with a pneumatophore and the sail (Fig. 69C-D) are also referred to as rataria larva. For more details see Woltereck (1904) and Leloup (1929).

Dimensions: Clony size depends on age and likely also genetic background, reaching maximal sizes of to 10 x 5 cm, but usually remaining much smaller. In the Mediterranean, the size is generally smaller than 4.5 x 2.1 cm. Also relatively small colonies (1 cm) can release medusae. Newly liberated medusae are about 1.2 mm high and 1 mm wide. Mature medusae from the plankton are up to 2.8 mm high and 2 mm wide (Larson, 1984). For nematocyst measurements see Weill (1934), Russell (1939), Bouillon (1978a), Calder (1988), and Schuchert (1996).

Other data: For more details on the nervous system see Carré (1979) and Mackie *et al.* (1988).

Biology: The hydroid colonies can occur in enormous swarms spreading over many kilometres and comprising hundreds of millions of animals (e. g. Flux, 2007). Such swarms are especially spectacular when stranded on beaches (e. g. Kemp, 1986).

Velella is predated upon by several opisthobranchs, especially so by *Glaucus atlanticus* Forster and *Janthina janthina* (L.) (see e. g. Bayer, 1963; Arai, 2005).

The two mirror-symmetric forms have different sailing properties and prevailing wind directions may sort them into groups in which one form dominates. The distribution pattern of the two forms was examined by Edwards (1966). Francis (1991) investigated the sailing performance of *Velella*.

For unknown reasons, the medusa has been collected very rarely, although it seems to be epipelagic (Larson, 1980). Brinckmann (1964) found that the medusae do not feed for the first five days. The animals are likely able to live solely on nutrients provided by the symbiotic algae. This atrophic period can be extended up to 30 days. The maturation of the gonads, however, is inhibited in non-feeding animals. The maturation gonads when feeding takes 20-24 days, this independent of the duration of the preceding atrophic period.

In the Mediterranean, the polyp colonies are strictly seasonal, occurring in winter and spring only (Brinckmann-Voss, 1970).

Distribution: Circumglobal in tropical to temperate waters. In the Atlantic recorded from 62°N (Norway) to 54°S (Edwards, 1966), also common in the Mediterranean. Type locality: Linnaeus (1758) based his description on accounts of earlier authors, of which only one gave a locality, namely Mediterranean Sea. According to article 76.1 of the ICZN, the type locality of *Medusa velella* Linnaeus, 1758 is thus the Mediterranean.

Remarks: *Velella* – like *Porpita* – is a relatively complex organism (Figs 65, 68). More details, and also other pertinent information and more references, can be found in e. g. Huxley (1858), Agassiz (1883), Bigelow (1911), Hyman (1940), Totton (1954), Brinckmann-Voss (1970), Kirkpatrick & Pugh (1984), and Calder (1988).

Family Rosalindidae Bouillon, 1985a

Diagnosis: Hydroid colonial; hydrorhiza crust-like, consisting of a basal layer of chitinous periderm from which rise spines and ridges, ridges may be elevated to a system of convoluted walls interconnected by trabeculae, basal periderm overlain by a layer of coenosarc and a filmy top-layer of periderm, spines may penetrate the coenosarc, coenosarc strands penetrate into the elevated parts of the basal periderm. Hydranths sessile or nearly so, club-shaped, with scattered capitate tentacles. Cnidome comprising stenoteles and macrobasic heteronemes.

Gonophores where known developing singly among lower tentacles, released as medusae with two tentacles, these reportedly provided with cnidophores like in *Zanclea*.

Remarks: The scope of the family as given above comprises only the genus *Rosalinda*. Petersen (1990) included *Rosalinda* together with *Teissieria* Bouillon, 1978b and *Pseudosolanderia* Bouillon & Gravier-Bonnet, 1988 in the same family Teissieridae Bouillon, 1978b, while Bouillon *et al.* (2006) kept all three genera in separate families. The relationships of the three genera are not well resolved (see also discussion in Bouillon & Gravier-Bonnet, 1988), and because all *Rosalinda* species are only incompletely known, it seems preferable for the moment to use the classification of Bouillon *et al.* (2006).

Genus ***Rosalinda*** Totton, 1949

Rosalinda Totton, 1949; type species: *Rosalinda williami* Totton, 1949 by monotypy.

Diagnosis: As for the family.

Key to species of *Rosalinda* of the ERMS zone:

1a growing on spider crab *Anamathia*, hydrorhiza thin, with isolated spines and ridges . . . . *R. incustans*

1b on non-mobile substrata, perisarc of hydrorhiza a spongy meshwork of convoluted ridges . . . . *R. williami*

Rosalinda incrustans (Kramp, 1947) Figs 70-71

Halocharis incrustans Kramp, 1947: 3, figs 1-5.

Rosalinda incrustans. – Picard, 1957: 7. – Prévot, 1959: 107, pl. 4 fig 15. – Vervoort, 1962: 538. – Vervoort, 1966: 383, figs 3D-F, 6-7. – Bouillon *et al.*, 2004: 112, fig. 58A-C.

Material examined: IRSNB, without specimen number; Mediterranean, Spain, Rosas, colonies on four *Anamathia* spider crabs, collected December 1958, det. J. Picard, leg. J. Bouillon, infertile. – MHNG INVE 39465; Mediterranean, west of Corsica, 42.355°N 09.611°W, 660-820 m, collected 01.11.1958, infertile colonies on several *Anamathia rissoana*.

Diagnosis: *Rosalinda* species growing on spider crab *Anamathia rissoana*, hydrorhiza thin, with isolated spines and ridges.

Description: Hydroid colony with continuous, crust-like hydrorhiza covering carapace and spines of spider crab. Hydrorhiza formed by a layer of coenosarc on a perisarc lamella and covered by membranous perisarc. Coenosarc transparent, with external epithelium enclosing the internal, anastomosing gastrodermal tubes; nematocysts in epidermal layer. Basal perisarc lamella usually with a cellular, roughly

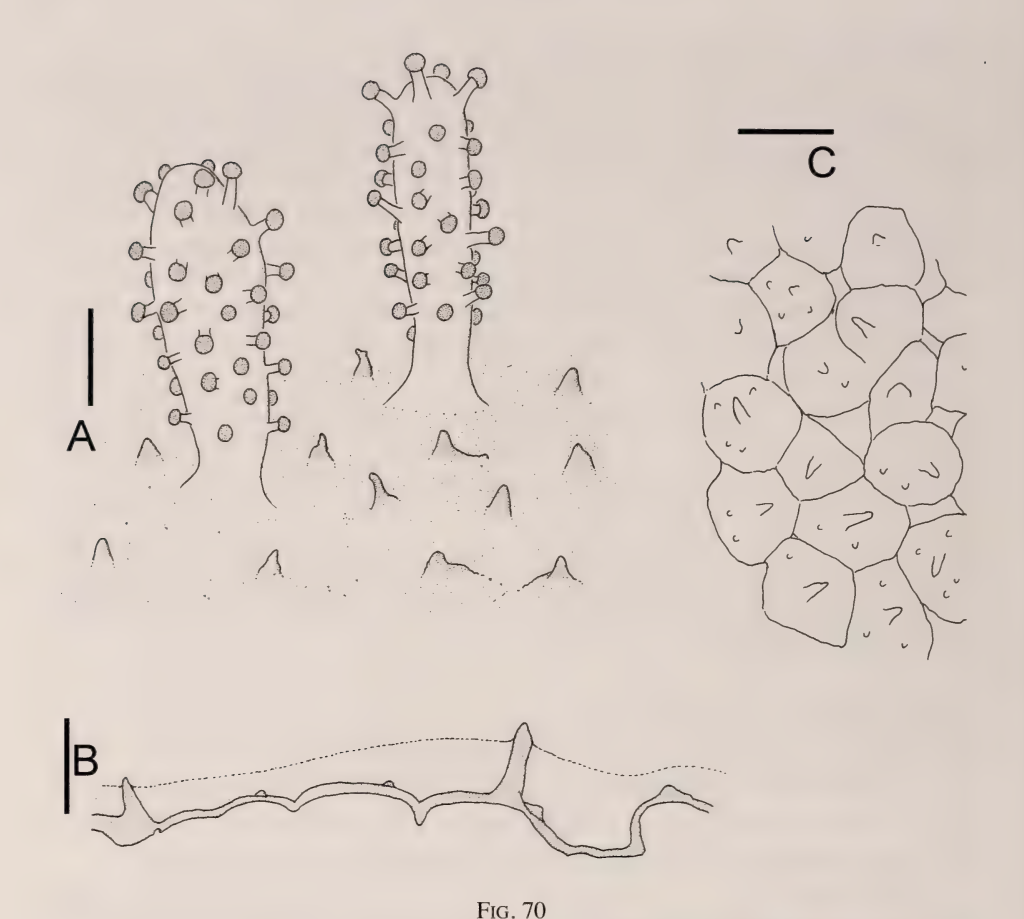


FIG. 70

Rosalinda incrustans (Kramp, 1947); after preserved material from the Mediterranean. (A) Two hydranths and the surrounding hydrorhiza crust; scale bar 0.5 mm. (B) Schematic vertical section of the hydrorhiza, the perisarc is stippled dark, the overlaying coenosarc light, note the spines penetrating the coenosarc; scale bar 0.1 mm. (C) Schematic sketch of a horizontal view of the perisarc, the spines are flattened due to the compression of the cover slip; scale bar 0.2 mm.

polygonal structure due to adnate, blister-like cupolas that are formed by moulding of the perisarc onto the surface structure of the crab integument. Each cell usually bears on its upper side a central perisarc spine of variable height, some scattered, smaller, wart-like processes, and sometimes also spiny ridges along the cell borders. Locally the perisarc can be thicker and with more ridges and spines. The spines often transverse and overtop the coenosarc layer.

Hydranths rather dense, club-shaped, sessile, diameter slightly narrowing near base than broadening again; with 30-50 capitate tentacles, short, no distinct oral whorl.

Nematocysts: Large and small stenoteles (the latter mostly in the tentacles), very large macrobasic heteronemes (mastigophores or euryteles with faint swelling of shaft), ? isorhizas.

Sexual reproduction unknown.

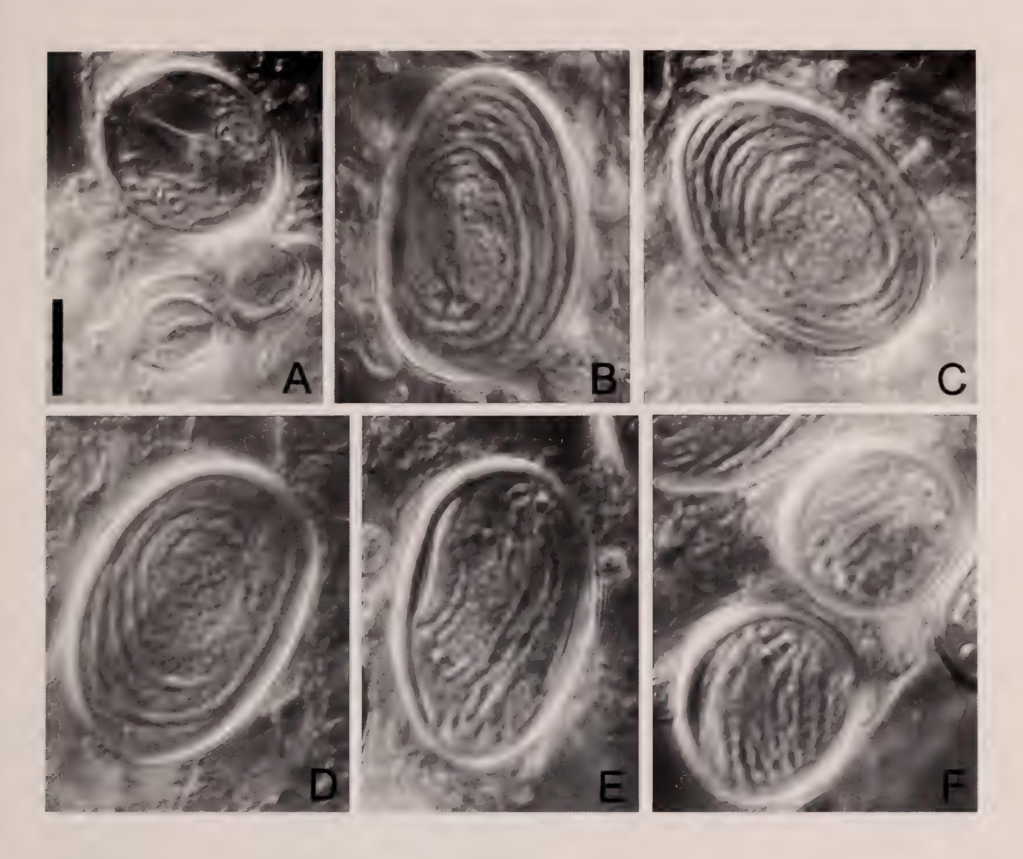


FIG. 71

Rosalinda incrustans (Kramp, 1947); nematocysts of sample MHNG INVE 39466, scale bar 10 μm. (A) Two types of stenoteles. (B-D) Macrobasic heteroneme in side view. (E) Macrobasic heteroneme, focused in centre region. (F) Macrobasic heteroneme, view perpendicular to long axis of capsule.

DIMENSIONS: Hydranths 1.5-3 mm (Vervoort, 1966). Preserved nematocysts: large stenoteles (20.5-21.5)x(17-18)μm; small stenoteles (9-10.5)x(7-8)μm; macrobasic heteroneme (32-34.5)x(23.5-25)μm; ?isorhizas reported by Vervoort (1966) (8)x(18)μm.

ADDITIONAL DATA: Prévot (1959) examined the histology of the hydranth and hydrorhiza. The tentacles are not separated from the gastrodermal cells by a mesogloeal layer. *Rosalinda* thus lacks morphologically distinct oral tentacles as seen *e. g.* in the polyps of *Zanclea*. For this respect, *Rosalinda* resembles more *Solanderia* and *Millepora*. Some aggregations of nematocysts around the mouth suggest that the oral tentacles of *Rosalinda* have been reduced.

BIOLOGY: Occurs epizoic on the deep-sea spider crab *Anamathia rissoana* Roux, living in depths of 225-820 m. For more details on *Anamathia* see e. g. Guerao & Abelló (1996) or Mura *et al.* (2005) and references herein.

Distribution: Atlantic Ocean, west of Gibraltar; western Mediterranean (Costa Brava and Corsica) (Kramp, 1947; Picard, 1957; this study). Type locality: off SW of Portugal, 36.667°N 14.250°W, 225 m, on *Anamathia rissoana* Roux.

Remarks: *Rosalinda incrustans* and *R. williami* are perhaps conspecific. Both nominal species are kept separate based on the structure of the perisarc and also differences of the cnidome. The structure of the perisarc of *R. incrustans* is largely determined by the moulding of the periderm onto the surface structure of the host carapace (Picard, 1957; Fig. 70C). The central spine which is usually present in each cell is due to a seta of the crab overgrown by thickened perisarc. This suggests that when occurring on other substrata, the hydrorhizal skeleton might thus look quite different, provided that *R. incustans* is not strictly host specific. The different hydrorhizal structure seen in *R. williami* could thus be due to the different substrate the original type specimen was growing on. A further difference of the two species was reported by Vervoort (1966): he found putative isorhiza-type nematocysts in *R. incrustans* which were apparently absent in *R. williami*. The type of the capsule could not be determined reliably as no discharged capsules were found, but their size made them clearly distinct from the larger heteronemes. I was unable to find this type of capsule (Fig. 71A-F), despite examining several colonies of unambiguously identifiable *R. incrustans* from two Mediterranean localities. Also Picard does not list this type of capsule. Perhaps this capsule is only produced in colonies with imminent development of gonophores, or there is more than one species involved. Because also the gonophores of *R. incrustans* and *R. williami* remain unknown, it is preferable not to synonymize them. It is still possible that both morphotypes might prove to have different life cycles.

Rosalinda williami Totton, 1949 Fig. 72

Rosalinda williami Totton, 1949: 45, figs 3-4. – Vervoort, 1962: 538. – Vervoort, 1966: 377, figs 1A, 2, 3A-B, 4, 5.

Type material examined: BMNH 1949.1.20.4; holotype and part of the same colony as paratype; in bad condition, no intact hydranths left, only some few mesogloeal residues of hydranths left.

Diagnosis: *Rosalinda* species growing on non-mobile substrata, perisarc of hydrorhiza a spongy meshwork of convoluted ridges and walls.

Description (Totton, 1949; Vervoort, 1966; own observations): Colony relatively large, growing on worm tubes or solitary coral. Hydrorhiza crust-like, formed by coenosarc and a basal perisarc skeleton. Coenosarc transparent, with external epithelium enclosing the internal, anastomosing gastrodermal tubes; nematocysts in epidermal layer. The basal perisarc skeleton is formed by a periderm membrane from which rise chitinous ridges or walls forming convoluted patterns, the upper part of these walls irregularly shaped and produced into spines and trabecules connecting to other walls, resulting in a sponge-like perisarc crust. The coenosarc penetrates as worm-like strands into the lacunae and between the perisarc walls. Scattered, slight depressions where the height of the perisarc walls is reduced are the attachment sites of the hydranths.

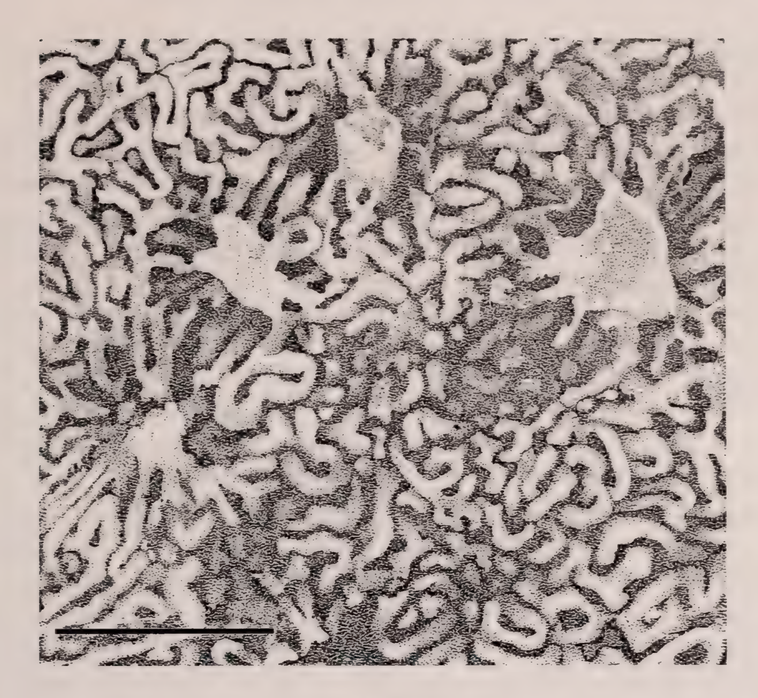


FIG. 72

Rosalinda williami Totton, 1949; from Vervoort (1966). Surface of the hydrorhiza with its convoluted perisarc ridges (dark) and coenosarc (bright). The hydranth attachment sites and their reduced height of the perisarc ridges are recognizable as larger, bright areas of coenosarc. Scale bar 1 mm.

Hydranths relatively dense, club-shaped, with 30-40 scattered capitate tentacles.

Nematocysts: small and large stenoteles, very large macrobasic heteronemes (mastigophores), shaft when discharged more than four times the length of the capsule.

Colour: rose-red when living.

Sexual reproduction unknown.

DIMENSIONS: Colony size up to 20 cm, hydrorhiza thickness 0.5 mm to a few mm, hydranths up to 2.65 mm high (Totton, 1949). Stenoteles 9x13μm and 18x25μm, mastigophores 24x36μm (Vervoort, 1966).

BIOLOGY: Deep water species, found growing on soft tubes of sedentary polychaetes, solitary corals, and perhaps also the calcareous axis of the gorgonian *Isidella elongata* (Tyler & Zibrowius, 1992).

DISTRIBUTION: Bay of Biscay. Type locality: 47.716°N 7.083°W, 438 m.

REMARKS: See under remarks for *R. incrustans*.

FAMILY ZANCLEIDAE RUSSELL, 1953

Orthocorynidae A. Agassiz, 1865; invalid name (Calder, 1988).

Corynipteridae Weill, 1934; invalid name (Calder, 1988).

Zancleidae Russell, 1953.
Halocorynidae Picard, 1957.

DIAGNOSIS: Hydroids colonial, polyps issued from creeping stolons, sessile or with usually unbranched pedicel; polyps monomorphic or polymorphic; gastrozooids either with oral and aboral capitate tentacles, or with reduced capitate tentacles, or without tentacles; gonozooids and dactylozooids, when present, with capitate tentacles or these reduced to variable degrees. Perisarc enveloping hydranth pedicels and stolons a simple tube and not lamellar.

Medusa umbrella bell-shaped; four perradial exumbrellar nematocyst patches, these either oval, clavate, elongate or linear, usually containing stenoteles; mouth simple, circular, without oral tentacles; gonads usually as interradial pads on manubrium, rarely in a single mass encircling manubrium; four radial canals; marginal tentacles 0, 2 or 4, hollow, when present with numerous, long, stalked nematocytes (cnidophores) containing macrobasic euryteles; without ocelli.

REMARKS: The taxonomic history of this family was outlined by Calder (1988), but there is no consensus on the scope and subdivision of the family (see also Weill, 1934; Millard, 1975; Bouillon; 1985; Calder, 1988). Petersen (1990) – using a phylogenetic approach – included also the genus *Asyncoryne* Warren, 1908 in the Zancleidae, while others (Bouillon *et al*., 2006) kept this genus in the separate family Asyncorynidae Kramp, 1949. A preliminary molecular phylogeny suggests that *Asyncoryne* is indeed closer related to other Capitata genera than to *Zanclea* (Nawrocki *et al*., 2010). Therefore, a scope as given in Bouillon *et al*. (2006) is used in this study.

Also the subdivision of the family into genera is disputed. Bouillon *et al*. (2006) used three genera: *Zanclea* Gegenbaur, 1857, *Zanclella* Boero & Hewitt, 1992, and *Halocoryne* Hadzi, 1917. The arguments for this subdivision are given in Boero *et al*. (2000), primarily in response to the opinion of Schuchert (1996) claiming that these three genera should be merged into a single genus. I still think that the three genera cannot be reliably separated based on morphological characters alone, as they intergrade once all species are taken into consideration. Bouillon *et al*. (2006) separate *Zanclella* from *Zanclea* by the following two traits: "gastrozooid usually with reduced number of tentacles" and "medusa umbrella laterally compressed in tentacular plane". A laterally compressed medusa bell is certainly an apomorphy, but in the type species of *Zanclella*, *Z. bryozoophila*, the medusa is not laterally compressed (see Boero & Hewitt, 1992; Boero *et al*., 2000). The remaining character "reduced number of tentacles" is too gradual to be applied reliably. Thus, *Zanclella* must be regarded as a synonym of *Zanclea*. A proper evaluation of the genus *Halocoryne* is hampered by its reduction seen both in the polyp and the medusa phase. This is particularly encumbering in the medusa, where the absence of cnidophores in the type species *Halocoryne epi*zoica makes it difficult to relate it to genus to *Zanclea*. In addition, also the absence of macrobasic heteronemes in the polyps render this genus difficult. The other species of *Halocoryne* described in Boero *et al*. (2000) illustrate again the fact that they are only gradually different from *Zanclea*. Whatever, the status of these genera can only properly be evaluated based on a robust, comprehensive molecular phylogeny. Until such a study becomes available, and in order to maintain a certain nomenclatural stability, I suggest to keep the genus *Halocoryne* for the time being.

KEY TO THE ZANCLEIDAE GENERA PRESENT IN THE ERMS ZONE

1a feeding zooids with capitate tentacles . . . . *Zanclea*
1b feeding zooids reduced, without capitate tentacles . . . . *Halocoryne*

Genus ***Zanclea*** Gegenbaur, 1857

Acrochordium Meyen, 1834; name suppressed by the ICZN (1994), opinion 1752.
Mnestra Krohn, 1853; name suppressed by the ICZN (1994), opinion 1752.
Zanclea Gegenbaur, 1857; type species *Zanclea costata* Gegenbaur, 1857 by monotypy, gender is feminine, placed on the Official List of Generic Names in Zoology by the ICZN (1994), opinion 1752.
Gemmaria McCrady, 1859, no type species designated.
Halocharis L. Agassiz, 1862, type species *Halocharis spiralis* A. Agassiz, 1862 by monotypy.
Gymnocoryne Hincks, 1871, type species *Gymnocoryne coronata* Hincks, 1871 by monotypy.
Zanlcea Allman, 1872: 290. [incorrect spelling]
Gemellaria Allman, 1872: pl. 7. [incorrect spelling]
Guentherella Weill, 1934, type species *Tubularia implexa* Alder, 1856b by monotypy.
Zanklea Riedl, 1963. [subsequent incorrect spelling]
Zanclella Boero & Hewitt, 1992, type species *Zanclella bryozoophila* Boero & Hewitt, 1992 by monotypy.

DIAGNOSIS: Colonial hydroids with stolonal hydrorhiza, polyps sessile or with pedicels, usually unbranched, polyps monomorphic or polymorphic, when polymorphic polyps may be differentiated into gastrozooids, gonozooids, and dactylozooids; gastrozooids elongated, cylindrical or claviform, always with capitate tentacles, tentacles usually numerous and scattered over body, in some species reduced to a few or a single tentacle; gonozooids and dactylozooids, when present, resembling reduced gastrozooids. Gonophores liberated as free medusae or rarely medusoids, newly liberated medusae with two opposite tentacles, umbrella bell-shaped, four exumbrellar perradial nematocyst patches or tracts containing stenoteles; four radial canals; two or four marginal tentacles when fully grown, tentacles with numerous abaxial extensile cnidophores containing macrobasic euryteles; mouth simple, circular; gonads interradial; no ocelli. Medusoids, if present, without tentacles or mouth, but usually with perradial exumbrellar nematocyst patches. Cnidome includes stenoteles and macrobasic euryteles, the latter type may be absent in the polyp stage.

REMARKS: Following the suggestion of Calder (1992), the ICZN validated the name *Zanclea* by placing it on the "Official List of Generic Names in Zoology" (ICZN, 1994). As discussed above, however, the scope of genus *Zanclea* remains unclear. For the taxonomic history of the genus see Calder (1988). The genus *Zanclea* was also discussed extensively in Weill (1934), Russell & Rees (1936), Russell (1953), and Gravili *et al.* (1996). Russell (1953) thought that there is only one *Zanclea* species in the European seas, namely *Z. costata* and most authors followed his authority in the following decades. However, it became clear that Russell's scope comprises more than one species (Picard, 1957; Boero *et al.*, 2000). The latter authors provided a synthesis of our current knowledge on the genus.

Zanclea medusae remain not reliably identifiable with our current knowledge. The 16S data of the more securely identifiable polyps (Fig. 73) could help in future to find diagnostic characters for some of them (see below).

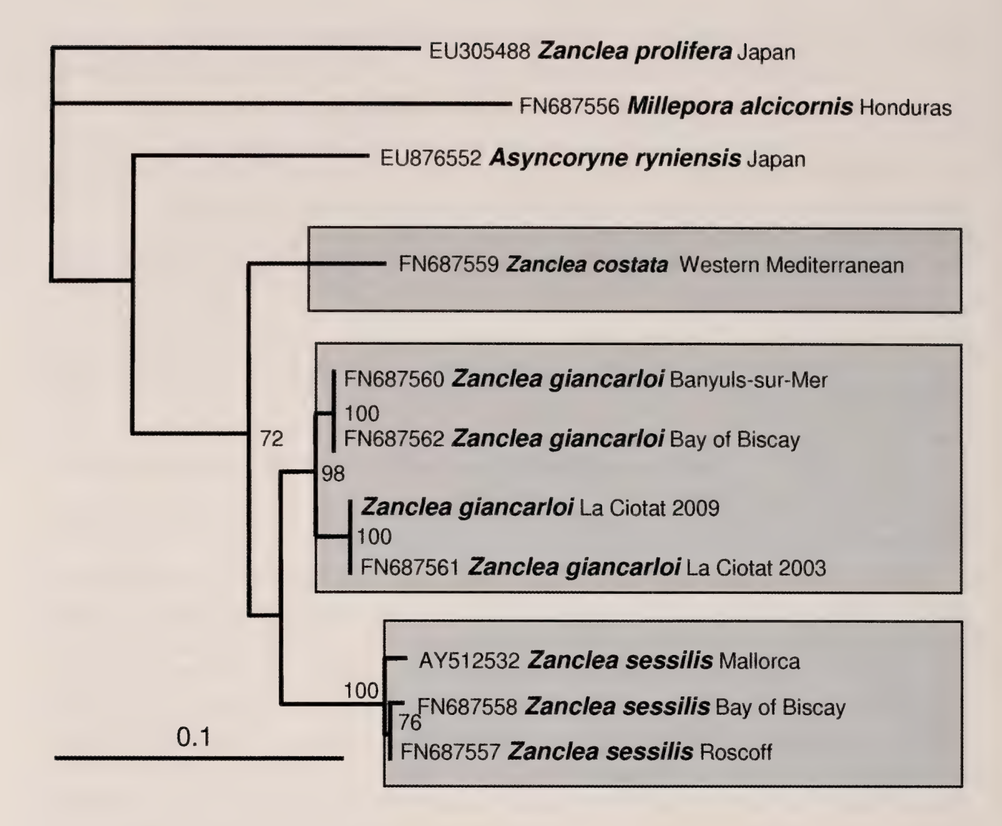


FIG. 73

Phylogenetic tree as graphic representation of 16S DNA sequences divergences of *Zanclea* samples examined in this study (569 bp, HKY model, maximum likelihood tree with % bootstrap support for each node (100 replicates), see Material and methods).

For the discussion of the synonymy of the species, I excluded all nominal species with type localities outside the ERMS zone. For biogeographic reasons they are all potentially valid and require careful nematocyst and life-cycle observations in order to assess their status. Likewise, all records of *Z. costata* and *Z. implexa* from regions outside the region of the northeastern Atlantic and Mediterranean are doubtful and should be scored as *Zanclea* spec. only. The status of all these *Zanclea* populations must likewise be re-evaluated using nematocyst and life-cycle studies (see Boero *et al.*, 2000).

MOLECULAR DATA: The partial 16S sequences of some *Zanclea* specimens of this study were used to examine their distinctiveness at the genetic level (comp. also Fig. 1). DNA samples were available for only three species and the number was relatively small, thus the results can only be seen as a pilot examination (Fig. 73). *Zanclea costata*, *Z. sessilis*, and *Z. giancarloi* were rather well separated, thus confirming their validity. The minimal observed interspecific distances, measured as % sequence differences, was 4.4%, while the maximal intraspecific distances were 1.4% for *Z. ses-*

TABLE 1. Characteristics of *Zanclea* species of the ERMS zone. More important traits in bold.

character	*Z. sessilis*	*Z. costata*	*Z. implexa*	*Z. giancarloi*	*Z. alba*
polyp distribution	Mediterranean to Norway	Mediterranean	**North Sea**	Mediterranean to Bay of Biscay	**Azores**, warm temperate Atlantic
substrate	living cheilostomate **bryozoans**	shells of living **bivalves**	**variable**, including rock old shells, manmade objects and hydroids	**various** substrates, Bryozoa and algae	floating ***Sargassum***
hydranth size in nature	1-1.5 mm	**2-5** mm	0.5-1 mm	1-1.5 mm	up to 1.6 mm
perisarc-covered pedicel	**absent or very short** in colonies from nature	present, long	present, long **may be branched**	present, perisarc filmy	present, perisarc thin
macrobasic euryteles	on hypostome, telotrichous, visible shaft with one coil in intact capsule	**holotrichous**, visible shaft with about 3 coils in intact capsule	on hypostome, telotrichous, visible shaft with 1.5 coils in intact capsule	among tentacles and on hypostome, telotrichous, visible shaft with 1-1.5 coils in intact capsule	**absent**
microbasic mastigophore	absent	**present**	absent	absent	absent
tentacles of medusa-budding hydranths	**strongly reduced**	not or only slightly reduced	not or only slightly reduced	not or only slightly reduced	not or only slightly reduced
linear swellings of radial canals of young medusa	yes	no	no?	no	no
tentacle number of mature medusa	2, perhaps also 4	2-4	unknown	2	unknown
life duration of medusa	> 1 month	> month	unknown	< 1 week	unknown

silis and 1.6% for *Z. giancarloi*. Species identification using 16S data could thus work well for these species and might be particularly helpful to identify the morphologically identical young medusa stages.

KEY TO SPECIES OF ZANCLEA OF THE ERMS ZONE

1a	polyps in nature with perisarc-covered pedicel 2
1b	polyps in nature without or with very short perisarc-covered pedicel, on Bryozoa only . . . . *Z. sessilis*
2a	polyps 2-3 mm, on shells of living Bivalvia, with microbasic mastigophores . . . . *Z. costata*
2b	polyps < 2 mm, on various substrates, without microbasic mastigophores . . . 3
3a	polyps on floating *Sargassum*, without macrobasic euryteles . . . . *Z. alba*
3b	polyps on various substrates, with macrobasic euryteles 4
4a	found in North Sea and Norwegian Sea . . . . *Z. implexa*
4b	Mediterranean and Bay of Biscay . . . . *Z. giancarloi*

Zanclea sessilis (Gosse, 1853) Figs 74-75

Coryne sessilis Gosse, 1853: 208, pl. 14 figs 1-3.
Gymnocoryne coronata Hincks, 1871: 76, pl. 5 figs 1, 1a.
Zanclea implexa. – Hincks, 1872: 393. – Russell & Rees, 1936: 107, figs 1-12. [not *Zanclea implexa* (Alder, 1856)]
? not *Corynitis agassizii*. – Murbach, 1899: 354, pl. 34 fig. 12. [not *Corynetes agassizi* (McCrady, 1859)]
? *Gemmaria implexa*. – Browne, 1905: 750.
? *Zanclea costata*. – Russell, 1938a: 420. – Russell, 1953: figs 43-48, pl. 4 figs 1-4. – Rees, 1952: 4.
Zanclea costata. – Russell, 1938b: 151, figs 19-22. – Brinckmann-Voss, 1970: 73, figs 85-87, pl. 4 figs 1. – Gravili *et al*., 1996: 103. [not *Zanclea costata* Gegenbaur, 1857]
? *Zanclea implexa*. – Buchanan, 1957: 352, fig. 3.
? *Zanclea sessilis*. – Millard & Bouillon, 1973: 21.
Zanclea sessilis. – Gravili *et al*., 1996: 101, figs 1-2. – Boero *et al*., 2000: 95, fig. 2. – Bouillon *et al*., 2004: 114, fig. 59J-M.
Zanclea cf. *alba*. – Vervoort, 2006: 200, figs 1a-b, 2.1-3. [not *Zanclea alba* (Meyen, 1834)]

MATERIAL EXAMINED: MHNG INVE 61438; English Channel, France, Roscoff; 06.05.2008, 70 m depth; on *Cellepora pumicosa*; colony cultivated, initially stolons completely embedded, in culture they get superficial and at base of hydranths there is a short delicate perisarc envelope of the pedicel, sometimes with annulation; medusae developed in August; 16S partial sequence accession code **FN687557**. – Mediterranean, Spain, Mallorca, Cala Murada; depth 3 m; 17.08.2000; cultivated; material not preserved; 16S partial sequence accession code **AY512532**. – Atlantic, Spain, San Sebastián (Guipúzcoa); collected, cultivated and identified by Dr Alvaro Altuna in August 2006; growing on bryozoa growing on *Cystoseira tamariscifolia*; material not preserved; 16S sequence **FN687558**.

DIAGNOSIS: *Zanclea* hydroid growing on cheilostomate Bryozoa; colonies from nature without or with only a very short perisarc-covered pedicel; large telotrichous macrobasic euryteles concentrated around hypostome and among oral tentacles, visible part of shaft in intact capsule in a single loop; medusa budding hydranths with reduced tentacles; medusa with elongated swellings of middle region of radial canals, fully grown medusa up to 3 mm high, with two tentacles, perhaps also four.

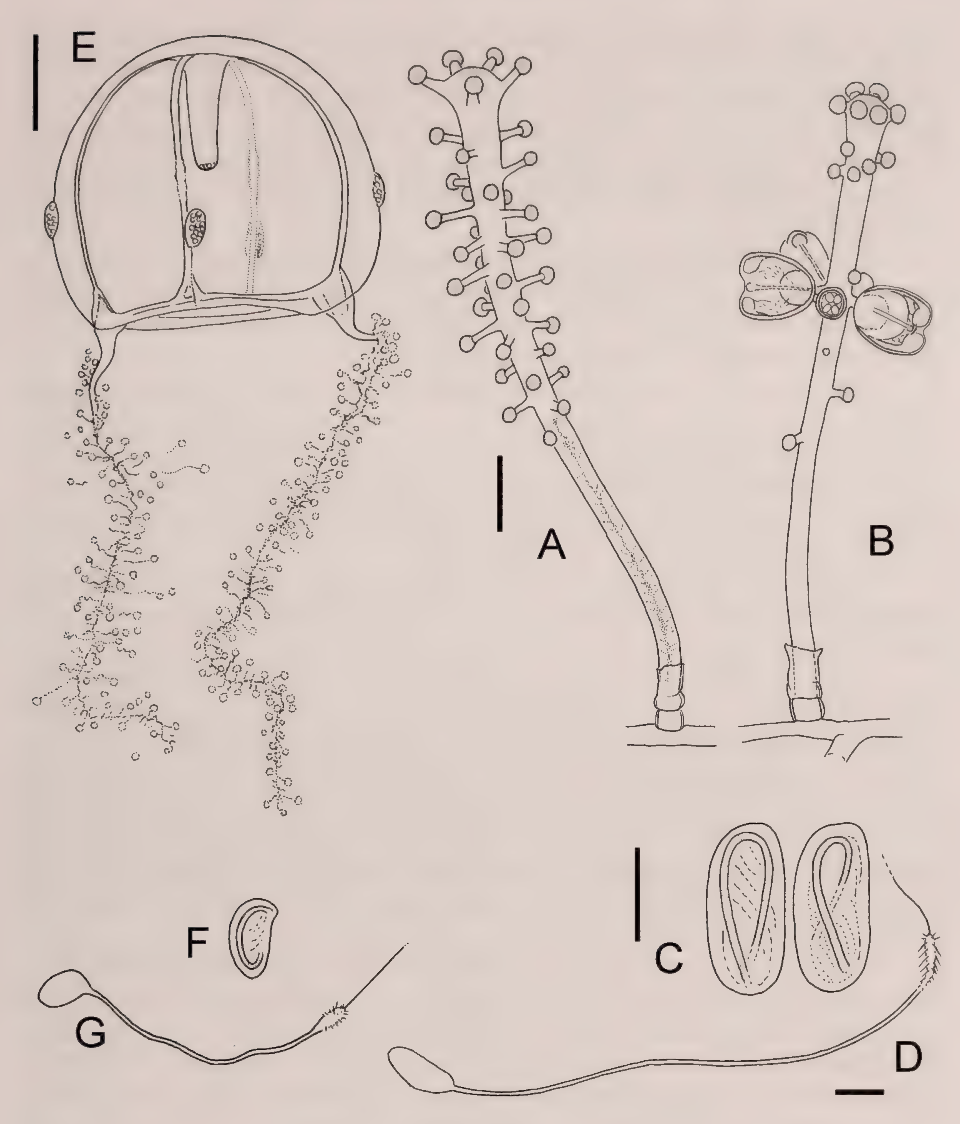


FIG. 74

Zanclea sessilis (Gosse, 1853); after living, cultivated material from Roscoff. (A) Hydranth without medusa buds, note that the basal perisarc covering of the stem was seen only in culture; scale bar 0.2 mm. (B) Polyp with medusa buds, the tentacles are partially reduced (= reproductive exhaustion), same scale as A. (C) Two intact macrobasic euryteles of the polyp hypostome, note the variation of the shaft loop; scale bar 10 μm. (D) Discharged telotrichous macrobasic eurytele; scale bar 10 μm (E) Newly liberated medusa; scale bar 0.2 mm. (F) Macrobasic eurytele from medusa nematophores; same scale as C. (G) Discharged macrobasic eurytele of medusa.

DESCRIPTION: Hydroid occurring in nature only on the surface of various cheilostomate bryozoan species, occasionally also colonizing its neighbouring substrate. Colonies in nature usually small, comprising a few hydranths, stolons creeping,

branched, may be partially embedded in bryozoan colony. Hydranths often sessile and without pedicels, sometimes base of hydranth in a short perisarc tube; hydranths with a white, rather shallow hypostome surrounded by a whorl of 4-7 capitate oral tentacles, about 20 scattered capitate tentacles in upper half of hydranth, contractile, with rather thin stalk when extended. Around hypostome and among oral tentacles many large macrobasic euryteles, on rest of hydranth body among other tentacles such capsules only occasional.

In culture, the hydroid is able to colonize other solid substrates, the hydranths get much longer (up to five times), the tentacle number increases to 30-50, the hydranth base gets ensheathed in perisarc of variable length, initially it is membranous and then gets thicker, sometimes even developing annulations.

Gonophores are medusa buds, developing initially among tentacles on normal hydranths which reduce subsequently their tentacles (reproductive exhaustion), feigning thus polyp polymorphism, lowest tentacles usually reduced first and buds thus appearing to develop below tentacle zone, medusa buds (up to six) in a whorl in the middle of the hydranth but otherwise not clustered, each bud with a stalk, advanced bud with two pairs of unequally developed bulbs.

Nematocysts: two size-classes of stenoteles; large telotrichous macrobasic euryteles, visible part of shaft in intact capsule in one coil, shaped like horseshoe or the Greek letter alpha (α).

Newly liberated medusa almost spherical, on exumbrella four perradial, oval nematocyst buttons containing stenoteles. Manubrium simple, tubular, spanning about half of the subumbrellar cavity, mouth surrounded by some stenoteles, no gonads visible. Four radial canals, well visible, usually in middle region with somewhat irregular outline due to thickened walls. Radial canals end in four marginal bulbs, one opposite pair large, the other very small, large bulbs bearing long, tapering, contractile tentacles with up to 50 cnidophores, cnidophores all on one side of tentacles, contractile, each usually with three macrobasic euryteles (2-5 range) and rarely a stenotele, distally with very long cilia.

Mature medusa from plankton currently not reliably identifiable. Mature, cultivated medusa (Russell & Rees, 1936; Gravili *et al.*, 1996) similar to young ones but larger, exumbrellar nematocyst pads elongated to a linear swelling reaching from bulbs halfway up the bell, containing 16-20 capsules mostly in a single row. Manubrium reaching almost to velum level, male gonads in four interradial masses, female animals with few eggs (1-3 per interradius). Slight linear swelling in the middle region of the radial canals. Bulbs unequally developed, with red pigment spots. So far all cultivated mature medusae did not develop more tentacles than the original pair, these long, 12-13 times as long as height of umbrella, ribbon-like due to hundreds of long cnidophores.

Nematocysts of medusa: two size-classes of stenoteles; telotrichous macrobasic euryteles in cnidophores.

DIMENSIONS: Hydranth height in material from nature about 1-1.5 mm, diameter 0.15 mm, in culture larger (2-10 mm high; Russell & Rees, 1936; Brinckmann-Voss, 1970); hydrocaulus in culture 0.4-0.6 mm. Undischarged nematocysts of polyp: large stenoteles (10-12.5)x(10-11)μm; smaller stenoteles (7.5-8)x(5-6)μm; macrobasic

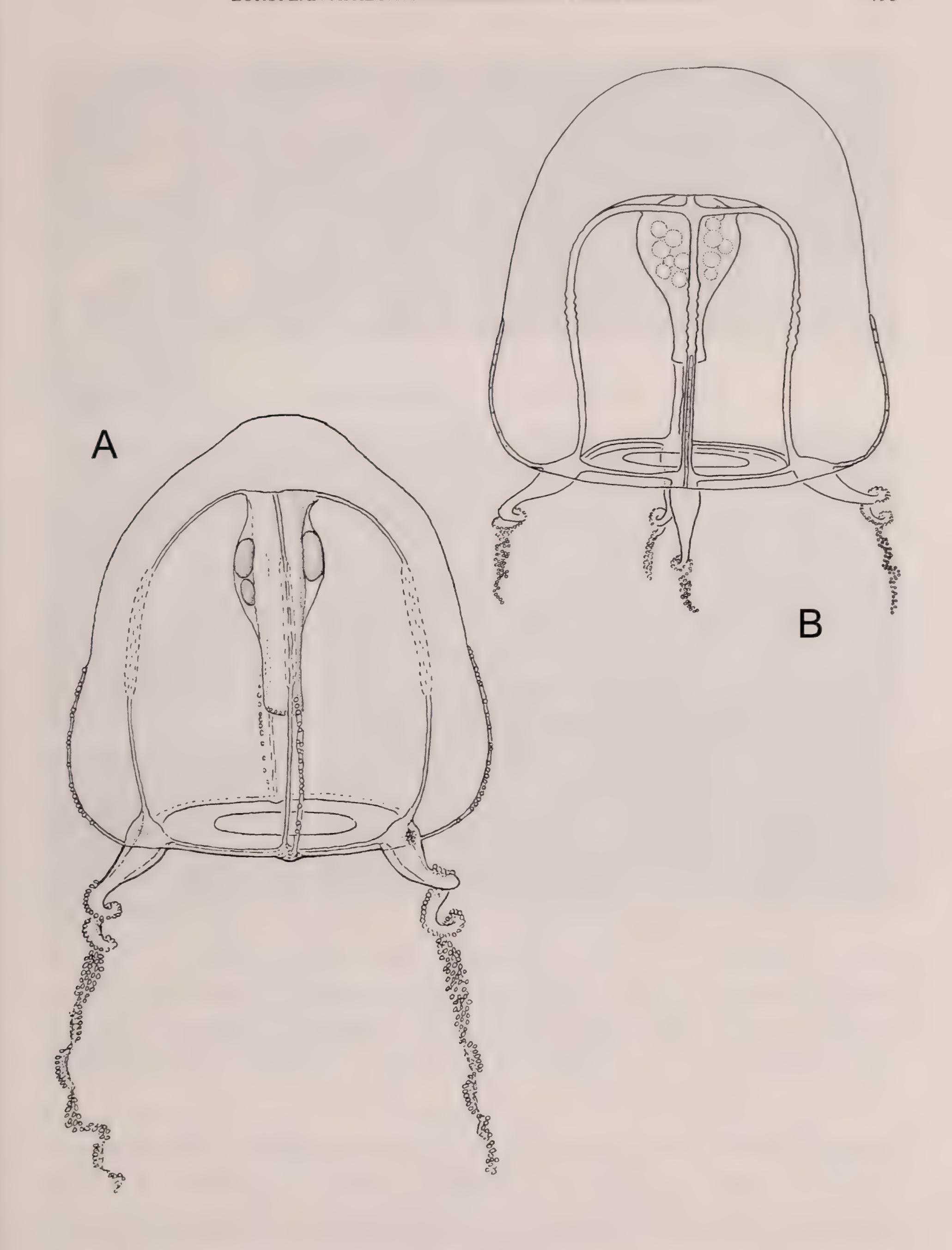


FIG. 75

(A) *Zanclea sessilis* (Gosse, 1853); mature medusa reared from hydroid stage, bell size about 1.4 mm; modified from Russell & Rees (1936). (B) ? *Zanclea sessilis*; mature medusa from the plankton, bell size 3 mm; modified from Russell (1953). Note that this medusa is only tentatively attributed to *Z. sessilis* due to the presence of the swellings along the radial canals. It is currently not known whether *Z. sessilis* may develop four tentacles like *Z. costata*.

euryteles (18-22)x(8)μm. Newly liberated medusae about 0.6-0.7 mm high (0.7-0.9 mm, Brinckmann-Voss, 1970; 0.4 mm Gravili *et al.*, 1996). In vitro, medusae reached heights of 1.4 mm (Russell & Rees, 1936) or 1 mm (Gravili *et al.*, 1996). In nature, the medusae probably get considerably larger (up to 3 mm; Russell, 1953; Brinckmann-Voss, 1970). Gonad maturation started at a height of 0.9 mm (Russell & Rees, 1936). Undischarged nematocysts of medusa: large stenotele (13-15)x(11-12)μm; smaller stenotele (8-8.5)x(6-6.5)μm; macrobasic euryteles (8-9)x(5-6)μm.

OTHER DATA: When disturbed, the hydranths bend back their distal part. A double-layered perisarc as described by earlier authors is due to regeneration (Russell & Rees, 1936).

BIOLOGY: Can be found growing on various bryozoans, e. g. *Cellepora pumicosa* (Pallas), *Turbicellepora avicularis* (Hincks), and *Beania* sp. Gosse (1953) originally reported it on *Lepralia*, a bryozoan genus of which most members have meanwhile been transferred to other genera. Depth range 1-60 m (Brinckmann-Voss, 1970). Medusa buds were observed from May to August (Teissier, 1965; Fey, 1970).

DISTRIBUTION: From northern Cornwall and the English Channel to the Iberian Penisula and the western and central Mediterranean (Gosse, 1853; Russell & Rees, 1936; Teissier, 1965; Fey, 1970; Brinckmann-Voss, 1970; Gravili *et al.*, 1996; this study). Perhaps reaching as far north as southern Norway (Rees, 1952, as *Z. costata*) and as far south as Ghana (Buchanan, 1957, as *Z. implexa*). Also reported from the Indian Ocean (Millard & Bouillon, 1973), but life-cycle studies must confirm the identity all records outside the ERMS zone. Type locality: Devon, Ilfracombe, Capstone Hill.

REMARKS: The studies of Gravili *et al.*, 1996 and Boero *et al.*, 2000 helped much in clarifying the status of *Z. sessilis* polyps and establishing it as a recognizable species. Earlier authors (e. g. Russell, 1953) incorrectly lumped all European *Zanclea* species into *Z. costata* (see Calder, 1988 and Gravili *et al.* (1996) for more details).

Boero *et al.* (2000) did not discuss the status of *Zanclea implexa* (Alder, 1857), perhaps implicitly following Russell & Rees (1936) who considered it as potentially conspecific with *Z. sessilis*. *Zanclea implexa* is here seen as distinct from *Z. sessilis* primarily based on two traits: (1) the natural occurrence on substrata other than Bryozoa and (2) on the constant presence of a perisarc covered pedicel, also in colonies taken from the sea. For more details see under *Z. implexa*.

Zanclea sessilis is only reliably identifiable in its polyp phase. The medusa liberated from *Z. sessilis* polyps has been cultivated to maturity by Russell & Rees (1936, as *Z. implexa*) and Gravili *et al.* (1996). In both cases, the medusa matured without developing a second tentacle pair, although their development was only followed up to a relatively small size. As hydromedusae often start reproduction before attaining their maximal size (Browne, 1905), it is well possible that in nature *Z. sessilis* medusae develop a second pair of tentacles as was observed for *Z. costata* (Brinckmann-Voss, 1970; as *Z. costata* var. *neapolitana*). Cultivated *Zanclea sessilis* medusae differed from *Z. costata* in having radial canals with linear swellings. This is perhaps a diagnostic trait for *Z. sessilis*, but unfortunately it is not known how reliable

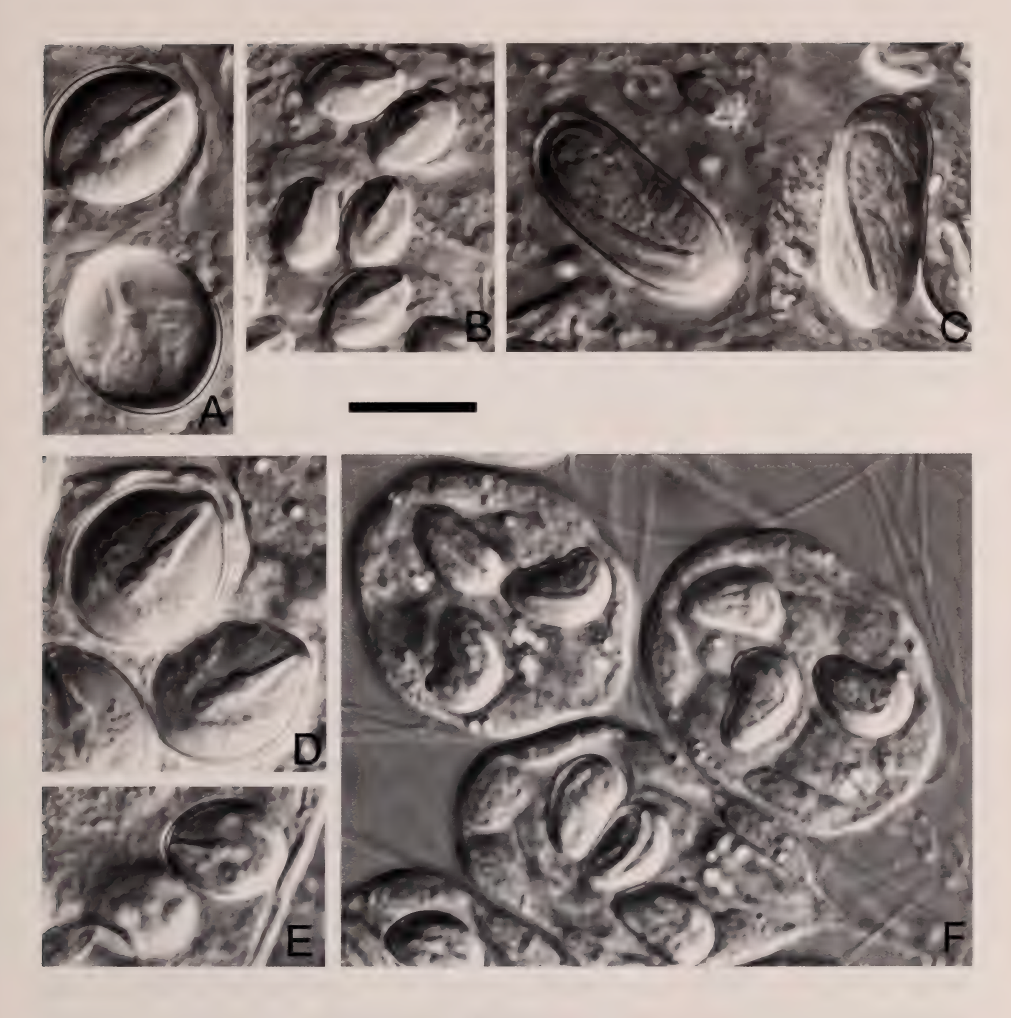


FIG. 76

Zanclea sessilis (Gosse, 1853); intact nematocysts of living polyp (A-C) and medusa (D-F); scale bar 10 μm. (A) Large stenoteles. (B) Small stenoteles. (C) Macrobasic euryteles. (D) Stenoteles of exumbrellar clusters. (E) Stenoteles of manubrium. (F) Nematophores with macrobasic euryteles.

this character is. Russell (1953, as *Z. costata*) depicts also a four-tentacled *Zanclea* medusa with such typical swellings (reproduced in Fig. 75B). This type of medusa is apparently quite common near Plymouth. Only the polyps of *Z. sessilis* are rather common in this region, while the polyps of *Z. costata sensu* Boero *et al*. (2000) or *Z. implexa sensu stricto* have never been found in the English Channel, or even nearby. I therefore suspect that *Z. sessilis* can also develop into four-tentacled medusae. The 16S DNA-sequences of *Z. sessilis*, *Z. costata*, and *Z. giancarloi* provided here (Fig. 73), permit the identification of medusae from the plankton and will hopefully settle the question in the near future.

Like many other *Zanclea* species (Boero *et al.*, 2000), *Z. sessilis* shows a close relationship with bryozoans, although it is not species specific. I think that the association with cheilostomate Bryozoa is a characteristic trait of this species, despite its ability to colonize other substrates in culture. Perhaps the larvae are only able to settle and metamorphose on Bryozoa, or young colonies are only able to survive in association with Bryozoa or the physical conditions they create in their surroundings. Experiments should be made to investigate this further.

Zanclea costata Gegenbaur, 1857 Fig. 77

Mnestra parasites Krohn, 1853: 281. – Martin & Brinckmann-Voss, 1963: 208, synoym.
Zanclea costata Gegenbaur, 1857: 229, pl. 8 figs 4-6. – Prévot, 1959: 110, pl. 4 fig. 21. – Martin & Brinckmann-Voss, 1963: 206, figs 1-15. – ICZN, 1994: 54. – Gravili *et al.*, 1996: 103, fig. 3. – Cerrano *et al.*, 1997: 177, figs 1-3. – Boero *et al.*, 2000: 97, fig. 3. – Bouillon *et al.*, 2004: 113, fig. 59A-D. – Peña Cantero & García Carrascosa, 2002: 47, fig. 9f-g.
? *Zanclea implexa*. – Du Plessis, 1881: 144.
Zanclea hargitti Hartlaub, 1907: 119, new name for *Gemmaria implexa* of Hargitt, 1904.
not *Zanclea costata*. – Mayer, 1910: 87, pl. 8 figs 2-3, 6-7. [= *Z. alba*]
Gemmaria implexa var. *neapolitana* Brückner, 1914: 460, figs 7-24, pl. 8 figs 3-15, pl 9 figs 16-25.
Gemmaria implexa. – Hargitt, 1904: 574, pl. 22 figs 27-29. [not *Zanclea implexa* (Alder, 1856)]
not *Zanclea costata*. – Russell, 1953: figs 43-48, pl. 4 figs 1-4. [= *Z. sessilis*]
not *Gemmaria costata*. – Naumov, 1969: 258, figs 52A, 127. [= *Z. implexa*]
Zanclea implexa var. *neapolitana*. – Brinckmann-Voss, 1970: 72, figs 83-84, pl. 4 fig. 1.
not *Zanclea costata*. – Brinckmann-Voss, 1970: 73, figs 85-87, pl. 4 figs 1. [= *Z. sessilis*]
? *Zanclea hargitti*. – Millard & Bouillon, 1973: 21.
not *Zanclea costata*. – Petersen, 1990: 141, fig. 12 A-B. [= *Z. implexa*]

MATERIAL EXAMINED: MHNG INVE 54653; Mediterranean, Italy, Naples, Cumes, collected 20.05.1889; on two *Chamelea gallina* each with a colony, with medusa buds. – MHNG INVE 26507; Mediterranean, France, Roussillon, beach near Sainte-Marie-la-Mer, depth 2-3 m, sandy bottom, several colonies on *Chamelea gallina* (L.), collected 15.07.1999, released medusae; one colony used for DNA extraction; accession numbers for 16S DNA sequence **FN687559**, 28S **EU879951**, 18S **EU876579**.

DIAGNOSIS: Large *Zanclea* hydroids growing exclusively on living, infaunal Bivalvia, with long, perisarc-covered pedicel and 70 or more tentacles; medusa buds distributed all over hydranth, tentacles not reduced in budding hydranths; with holotrichous macrobasic euryteles and microbasic mastigophores. Fully developed medusa with four tentacles, 2-5 mm, radial canals without linear swellings.

DESCRIPTION: Colonial hydroids growing exclusively on the upper part of shells of Bivalvia living partially embedded in the sediment. Colonies relatively large, comprising up to 70 hydranths issued from a creeping, branched stolon system, stolons and pedicel of hydranth covered with a brownish, corrugated or annulated perisarc which extends up to the lowest tentacles of the hydranth. Hydranths always with a long but unbranched pedicel covered with perisarc. Hydranths tall and elongated compared to other species of the genus, with 40-90 scattered tentacles, about 5-6 oral tentacles around the shallow hypostome.

Gonophores are medusa buds, developing within the tentacle zone, tentacles not much reduced in medusa-budding hydranths, buds scattered, up to 20 may be present, each bud with a stalk, advanced buds with two pairs of unequally developed bulbs.

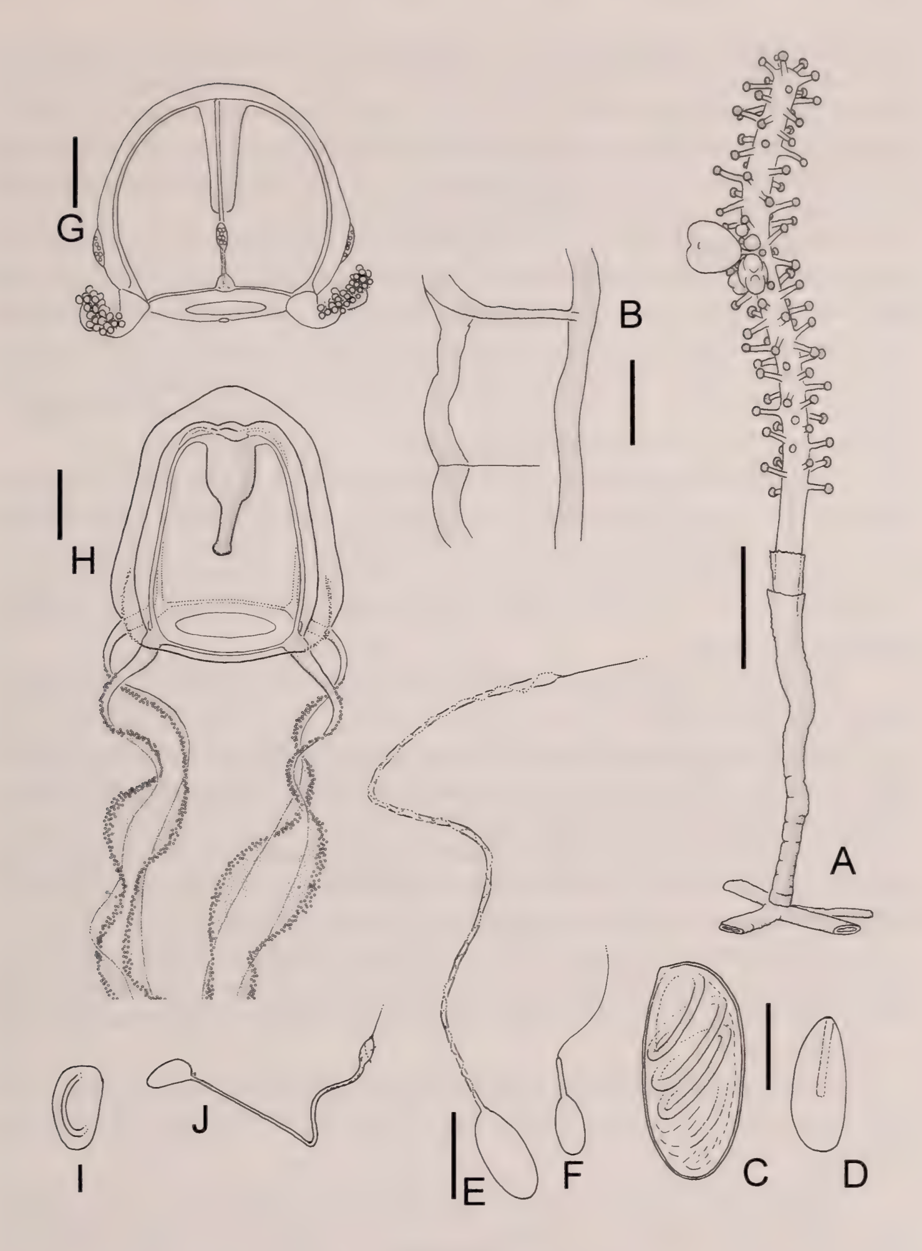


FIG. 77

Zanclea costata Gegenbaur, 1857; A-G, I-J after living and preserved material, H modified after Brinckmann-Voss (1970). (A) Polyp with medusa buds; scale bar 1 mm. (B) Perisarc of lower part of stem in lateral view; scale bar 0.1 mm. (C) Intact macrobasic eurytele of polyp; scale bar 10 μm. (D) Intact microbasic mastigophore of polyp; same scale as C. (E) Discharged macrobasic eurytele of polyp; scale bar 20 μm. (F) Discharged microbasic mastigophore of polyp; same scale as E. (G) One-day-old medusa; scale bar 0.2 mm. (H) Mature male medusa, ends of tentacles cut; scale bar 1 mm. (I) Intact macrobasic eurytele of medusa nematophores; same scale as C. (J) Discharged macrobasic eurytele of medusa; same scale as E.

Nematocysts: two size-classes of stenoteles; large holotrichous macrobasic euryteles, visible part of shaft in intact capsule in three or more oblique coils, discharged shaft about six-times as long as capsule; microbasic mastigophores in hydranth body and stolons. In colonies from nature only few macrobasic euryteles present in the hydranth body-wall and the stolons. In cultivated hydranths abundant in the hydrorhiza, hydranth body and above the oral tentacles.

Newly liberated medusa almost spherical, on exumbrella four perradial, oval nematocyst buttons containing stenoteles. Manubrium simple, tubular, spanning about half of the subumbrellar cavity, no gonads visible. Four radial canals, well visible, no linear swellings. Radial canals end in four marginal bulbs, one opposite pair large, the other very small, large bulbs bearing long, tapering, contractile tentacles with about 50 cnidophores, cnidophores all on one side of tentacles, contractile, each with usually 3-5 macrobasic euryteles, distally with long cilia.

Mature medusa (Gegenbaur, 1857; Brinckmann-Voss, 1970) bell-shaped, jelly slightly thicker at apex, exumbrellar nematocysts in linear, meridional tracks running from the bulbs upwards, length variable and depending on age. Fully grown with four or two tentacles bearing numerous cnidophores, all attached in a linear series, stalks of cnidophores variable, short proximal, longest distal. Gonads surround manubrium, females with > 10 eggs.

Nematocysts of medusa: two size-classes of stenoteles, telotrichous macrobasic euryteles in cnidophores.

DIMENSIONS: Hydranth pedicels 2-6 mm high, diameter 0.2-0.3 mm. Hydranth bodies in colonies from nature 2-5 mm, may reach 10-15 mm in cultivated animals (Brinckmann-Voss, 1970; Cerrano *et al.*, 1997).

Polyp nematocysts (preserved material, living material is 10-20% larger): large stenoteles (15.5-18)x(11.5-13.5)μm; small stenoteles (8-9)x(6-6.5)μm; macrobasic euryteles (21-27)x(11-14)μm; mastigophores (12-16)x(5.5-7.5)μm.

Medusa with four tentacles 2-5 mm in height, egg size 0.16 mm (Gegenbaur, 1857). Nematocysts of medusa (preserved material): large stenoteles on exumbrella (14-14.5)x(9-12)μm; smaller stenoteles from mouth (7)x(5)μm; macrobasic euryteles (11-12)x(6-7)μm.

Cerrano *et al.* (1997) observed larger capsules, especially the stenoteles of the polyp were considerably larger. Nematocyst sizes of hydrozoans can differ between populations.

OTHER DATA: The hydroid can be cultivated (Brinckmann-Voss, 1970; Cerrano *et al.*, 1997). The number of macrobasic euryteles increases in culture, especially among the oral tentacles. Brinckmann-Voss (1970) observed that the medusa develops a second tentacle pair between two weeks and one month of age, concomitantly with the gonad ripening. Cerrano *et al.* (1997) reared the medusa to maturity (1 month, bell size 2 mm), but his animals failed to develop a second pair of tentacles within the observation period.

Brückner (1914) describes in detail the histology of the polyp. Zoja (1895b) depicts the development of the polyp from the egg.

BIOLOGY: The hydroids can be found in rather shallow coastal waters (2.5-5 m, Brückner, 1914) growing on shells of Bivalvia which are partially imbedded in the sediment, preferentially on *Chamelea gallina* (L.), but it has also been found on *Spisula subtruncata* (da Costa), *Venus ovata* Pennant, and *Cardium* spec. (Brückner, 1914; Brinckmann-Voss, 1970; Peña Cantero & García Carrascosa, 2002). Medusa budding has been observed from May to August (Cerrano *et al.*, 1997). Medusae can be found in the plankton of the Bay of Naples from March through June, although at very low numbers (Brinckmann-Voss, 1987). The medusa swims vigorously and is extremely sensitive to light (Brinckmann-Voss, 1970). It can be parasitized by the nudibranch *Phylliroe bucephala* Péron & Lesueur. The parasitized form looses its tentacles and has been given its own name, *Mnestra parasites* (Martin & Brinckmann-Voss, 1963; Martin, 1966).

DISTRIBUTION: Endemic to the Mediterranean. Reliable records based on the polyp stage are from the Alborean Sea (Peña Cantero & García Carrascosa 2002), north-western Mediterranean (this study), the Ligurian Sea (Prévot, 1959; Cerrano *et al.*, 1997), Bay of Naples (Hargitt, 1904; Brückner, 1914; Brinckmann-Voss, 1970), Strait of Messina (Gegenbaur, 1857), and Apulia (Gravili *et al.*, 1996; Boero *et al.*, 2000). Type locality: Italy, Strait of Messina (medusa).

REMARKS: Gegenbaur (1857) introduced the name *Zanclea costata* for a Mediterranean medusa with four tentacles bearing characteristic nematophores. The four-tentacled medusae contrasted with subsequent observations of medusae released from *Zanclea* hydroids which always have two tentacles only. Browne (1905) then found both medusa types together in the same plankton catches and concluded that the four-tentacled medusae were only more advanced growth stages of the same species. Russell (1953) made similar observations and together with his earlier observations on the variability of the polyp stage (Russell & Rees, 1936), this must have led him to synonymize all European *Zanclea* species with *Z. costata* (erroneously assuming that this is the oldest available name). Later also Kramp in his influential monographs (1959, 1961) propagated this view and *Z. costata* soon became a catch-pool for various different morphotypes, including also nominal species that were entirely based on the polyp stage.

The first clearly recognizable *Zanclea* polyp was *Z. implexa* from the North Sea described by Alder (1856b, 1857a, 1857b, 1862), a nominal species which Russell (1953) also included in the synonymy of *Z. costata*. Hargitt (1904) described then a Mediterranean *Zanclea* polyp which he assigned to *Z. implexa*, but he already noted differences to Alder's descriptions. Hartlaub (1907: 119, footnote) considered these differences as important enough to give the Mediterranean form a separate name as *Z. hargitti*. The same morphotype was somewhat later described in detail by Brückner (1914) using the name *Gemmaria implexa* var. *neapolitana*. The studies of Brinckmann-Voss (1970) confirmed that contrary to Russell's view different species or subspecies of *Zanclea* polyps can be distinguished, notably the well defined morphotype of *Z. hargitti* seemed distinct from what is now known as *Z. sessilis*. Moreover, *Z. hargitti* indeed produced medusae which developed four tentacles. The studies of Gravili *et al.* (1996), Cerrano *et al.* (1997), and Boero *et al.* (2000) then decisively

shaped our current scope and taxonomy of the species *Z. costata* in particular, and the genus *Zanclea* in general. *Zanclea costata* is nowadays understood in the sense of *Z. hargitti* and it can produce medusae having two or four tentacles when mature. Although very plausible, the formal linking of Gegenbaur's medusa *Z. costata* with the hydroid *Z. hargitti* remains nevertheless somewhat arbitrary, as also other *Zanclea* hydroids – like *Z. sessilis* – could develop into four-tentacled medusae under natural conditions. Molecular analyses of four-tentacled *Zanclea* medusae from Messina could thus help to prove that our current concept of the species is correct, viz. that these medusae indeed belong to the polyp morphotype represented by the nominal species *Z. hargitti* (= *Z. implexa* var. *neapolitana*).

It is interesting to note that the polyp of *Z. costata* (= *Z. hargitti*) has never been found outside the Mediterranean, despite that it is rather conspicuous and its preferred host *Chamelea gallina* is a common species along the European Atlantic coast.

Zanclea alba (Meyen, 1834) Fig. 78

Acrochordium alba Meyen, 1834: 165, pl. 28 fig. 8.
Zanclea costata. – Mayer, 1910: 87, pl. 8 figs 2-3, 6-7. [not *Zanclea costata* Gegenbaur, 1857]
Zanclea alba. – Calder, 1988: 69, figs 51-52. – Boero *et al.*, 2000: 95, fig. 1. – Galea, 2008: 15.

Diagnosis: Occurring only on floating *Sargassum*, polyp lacks macrobasic euryteles.

Description (Calder, 1988): *Zanclea* colonies growing only on floating *Sargassum*. Hydranths issued from a creeping, branched stolon system, stolons and pedicels of hydranth covered with a thin perisarc which extends up to the base of the hydranth, corrugated or annulated at base of pedicels. Hydranths with a long, unbranched pedicel covered with thin perisarc. Hydranth size as for most other species of the genus, 40 or more scattered tentacles, 5-7 identical oral tentacles around shallow hypostome.

Gonophores are medusa buds, developing in a cluster in the lower part of the tentacle zone, with short stalks.

Nematocysts: two size-classes of stenoteles, macrobasic euryteles absent.

Newly liberated medusa with four perradial oval nematocyst patches containing stenoteles on exumbrella just above marginal bulbs. Manubrium simple, tubular, spanning about half of the subumbrellar cavity, no gonads visible. Four radial canals clearly visible, no linear swellings. Radial canals end in four marginal bulbs, one opposite pair large, the other very small, large bulbs bearing long, tapering, contractile tentacles with cnidophores, cnidophores all on one side of tentacles.

Adult medusa unknown.

Nematocysts of medusa: two size-classes of stenoteles; telotrichous macrobasic euryteles in cnidophores.

Dimensions (Calder, 1988): Pedicels up to 1.3 mm, 0.07 mm wide, hydranth up to 1.6 mm long, 0.15 mm wide. Polyp nematocysts: large stenoteles (9.5-10.5)x(8.5-9μm); small stenoteles (6.5-7)x(5-5.5)μm. Nematocysts of medusa: stenoteles (7-9)x(6-7.5)μm; macrobasic euryteles (6.5-7)x(3.5-4.5)μm.

Biology: Epiphytic on pelagic *Sargassum natans* seaweed.

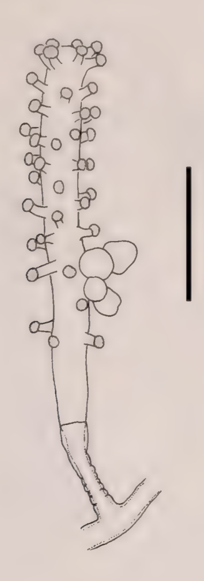


FIG. 78
Zanclea alba (Meyen, 1834); polyp with medusa buds; scale bar 0.5 mm; modified after Calder (1988).

DISTRIBUTION: Azores (Meyen, 1834), Bermuda (Calder, 1988), Florida (Mayer, 1910, as *Z. costata*). Type locality: Azores.

REMARKS: A distinct *Zanclea* species characterized through its occurrence on *Sargassum natans* seaweeds and the absence of macrobasic euryteles in the polyp (Galea, 2008).

Zanclea implexa (Alder, 1856) Fig. 79

Tubularia implexa Alder, 1856b: 439. – Alder, 1857a: 108, pl. 9 figs 3-6. – Alder, 1857b: 245. – Cornelius & Garfath, 1980: 276.
Coryne Briareus Allman, 1859: 55. – Allman, 1864a: 13. – Alder, 1862: 227, synonym. – Hincks, 1868: 59, synonym.
Coryne pelagica Alder, 1857a: 103, pl. 9 figs 1-2. – Alder, 1862: 227.
Coryne (*margarica* mihi) *implexa*. – Wright, 1859: 107, pl. 8 figs 6-7.
Gemmaria margarica Wright, 1859: 108. [invalid name]
Coryne implexa. – Alder, 1862: 227, pl. 10 fig. 4. – Bonnevie, 1901: 4, pl. 1 fig. 1.
Zanclea implexa. – Hincks, 1868: 59, pl. 9 fig. 3. – Allman, 1864b: 63.
Gemmaria implexa. – Allman, 1872: 290, pl. 7.
Gemellaria implexa. – Allman, 1872: legend to plate 7. [lapsus]
not *Zanclea implexa*. – Du Plessis, 1881: 144. – Jickeli, 1883: 611, pl. 26 fig 23-30. – Neppi, 1912: 719, pl. 2 fig. 4.
Zanclea implexa. – Swenander, 1904: 5. – Mayer, 1910: 89, figs 43-44.
not *Gemmaria implexa*. – Hargitt, 1904: 574, pl. 22 figs 27-29.
not *Coryne implexa*. – Motz-Kossowska, 1905: 46.
in part *Zanclea implexa*. – Hartlaub, 1907: 116, figs 106-108, 110-111.
not *Gemmaria implexa*. – Stechow, 1919: 5. [= *Slabberia halterata*]
Gemmaria implexa. – Stechow, 1925: 405, fig. 1. – Weill, 1934: 417.

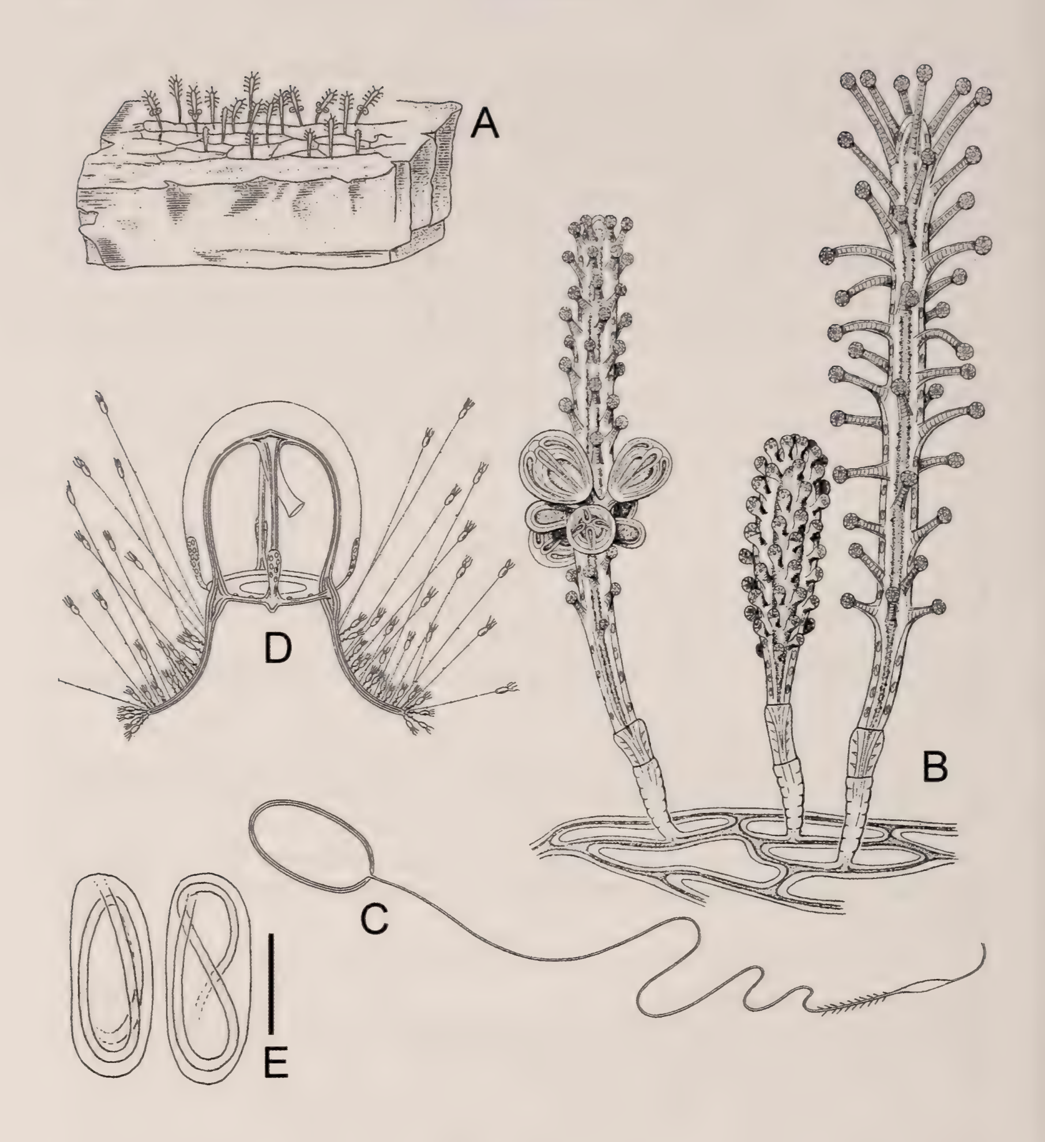


FIG. 79

Zanclea implexa (Alder, 1856b); A-D modified after Allman (1872), material from Scotland, E after preserved material from Sweden. (A) Colony growing on rock, natural size. (B) Three hydranths, left one with medusa buds. (C) Discharged macrobasic eurytele. (D) Newly liberated medusa. (E) Two macrobasic euryteles, note variability of shaft coiling; scale bar 10 μm.

? in part *Zanclea costata*. – Kramp, 1959: 94.
? not *Zanclea implexa*. – Rees & Roa, 1966: 39, fig. 1.
? in part *Gemmaria costata*. – Naumov, 1969: 258, figs 52A, 127.
Zanclea costata. – Petersen, 1990: 141, fig. 12A. [not *Zanclea costata* Gegenbauer, 1857]

MATERIAL EXAMINED: ZMUC, without registration number; Denmark, Frederikshavn; collected 09.07.1956; infertile hydranths on stems of *Tubularia indivisa*; det. P. L. Kramp as *Z. costata*; material also depicted in Petersen (1990). – GNM Hydrozoa 1442; Sweden, Kattegatt,

off Gothenburg; depth 46-63 m; collected 24.08.2006; colony on stem of *Tubularia indivisa*, large colony comprising several well preserved hydranths without medusa buds, some hydrocauli branched.

DIAGNOSIS: Occurring in northern North Sea to Norwegian Sea, growing on a variety of substrates and not exclusively on bivalves and Bryozoa, hydranth with long, perisarc covered pedicel, pedicel may be branched once, up to 50 tentacles per hydranth, ring of telotrichous macrobasic euryteles on hypostome. Radial canals of newly liberated medusa without linear swellings.

DESCRIPTION: *Zanclea* colonies growing on a variety of substrates and not exclusively on living bivalves and Bryozoa, e. g. on rock, old shells, man-made objects, and hydroids. Hydranths issued from a creeping, branched stolon system, stolons and stems of hydranth covered with a brownish, corrugated or annulated perisarc which extends up to the lowest tentacles of the hydranth. Hydranths always with a long, occasionally branched stem covered with perisarc, diameter of pedicel-perisarc widening somewhat from basal to distal. Hydranth size as for most other species of the genus, with 35-50 scattered tentacles, 5-7 oral tentacles around shallow hypostome. Above oral tentacles a dense ring of large macrobasic euryteles.

Gonophores are medusa buds, developing in a cluster in the lower part of the tentacle zone, tentacles not much reduced in medusa-budding hydranths, buds each bud with a stalk.

Nematocysts: two size-classes of stenoteles; large telotrichous macrobasic euryteles, visible part of shaft in intact capsule in 1.5 coils, coiling variable.

Newly liberated medusa almost spherical, on exumbrella four perradial, oval nematocyst patches containing stenoteles. Manubrium simple, tubular, spanning about half of the subumbrellar cavity, no gonads visible. Four radial canals clearly visible, no linear swellings. Radial canals end in four marginal bulbs, one opposite pair large, the other very small, large bulbs bearing long, tapering, contractile tentacles with cnidophores, cnidophores all on one side of tentacles, contractile, each with usually 3-5 macrobasic euryteles, distally with long cilia.

Mature medusa unknown.

DIMENSIONS: Hydranths 0.5-1 mm long, their perisarc covered pedicels up to 2 mm, diameter 0.13-0.17 mm.

OTHER DATA: Sometimes the pedicel has a double-layered perisarc, which is due to regeneration (Russell & Rees, 1936).

BIOLOGY: Grows on a variety of solid substrata, inlcuding rock, stems of *Tubularia indivisa*, dead shells, and man-made objects (old anchor). Allman (1872) reported it from tide pools, but otherwise more usually in 40-80 m depth.

DISTRIBUTION: A Nordic species, known from Northumbria and Scotland (Alder, 1857a-b; 1862; Wright, 1859; Allman, 1872); Denmark (Petersen, 1990; this study); Sweden (this study, and Norway (Bonnevie, 1901; Swenander, 1904). All – or most – other records are not trustworthy. Type locality: North Sea, England, Northumbria, thirty miles east of Holy Island.

REMARKS: *Zanclea implexa* is based on the polyp stage and is only incompletely known as the medusa has never been reared to maturity. The species has frequently

been confounded with *Z. sessilis*, most notably by Russell & Rees (1936). I think that *Z. implexa* is a valid species and distinct from both, *Z. sessilis* and *Z. costata*. The differences to *Z. giancarloi* are less obvious, but a full comparison is hampered by the lack of information on the mature medusa. Table 1 lists the differences for the *Zanclea* species occurring in the ERMS zone.

Zanclea giancarloi Boero, Bouillon, & Gravili, 2000 Figs 80-81

? *Gemmaria implexa*. – Jickeli, 1883: 611, pl. 26 figs 23-30.
? *Coryne implexa*. – Motz-Kossowska, 1905: 46.
Zanclea sp. Gravili, Boero & Bouillo, 1996: 104, fig. 4.
Zanclea giancarloi Boero *et al*., 2000: 100, fig. 9. – Bouillon *et al*., 2004: 113, fig. 59E-I.

Material examined: MHNG INVE 67059; aquarium culture of material from Banyuls-sur-Mer, Roussillon, France, summer 1991. – Mediterranean, France, Banyuls-sur-Mer, below "Village Catalan"; 0-2 m; collected 13.05.2002; colony growing on bryozoan, no medusa buds; not preserved, used to extract DNA; 16S sequence **FN687560**. – Mediterranean, France, La Ciotat; 0-2 m; collected October 2003; colony growing on algae, no medusa buds; collected and cultivated by Horia Galea, not preserved, used to extract DNA; 16S sequence **FN687561**. – Mediterranean, France, La Ciotat; collected September 2009; colony growing on algae; collected and cultivated by Horia Galea, not preserved, used to extract DNA; 16S sequence identical to previous sample from La Ciotat. – Atlantic, Spain, Fuenterrabía (Guipúzcoa); 4-8 m; collected November 2006; colony with medusa buds growing on bryozoan; collected and cultivated by Alvaro Altuna, not preserved, used to extract DNA; 16S sequence **FN687562**.

Diagnosis: Mediterranean to Bay of Biscay, growing on a variety of substrates such as bryozoans and algae, hydranth usually with pedicel, pedicel covered with thin perisarc and unbranched, 30-60 tentacles, not much reduced in medusa-budding hydranths; telotrichous macrobasic euryteles on hypostome and body, in intact capsule shaft in more than one coil. Radial canals of newly liberated medusa without linear swellings, medusa short-lived, mature with two tentacles only.

Description: *Zanclea* colonies growing on a variety of substrates, including Bryozoa and algae. Hydranths issued from a creeping, branched stolon system, stolons and stems of hydranth covered with a thin, brownish, corrugated or annulated perisarc which extends up to the lowest tentacles of the hydranth. Hydranths usually with a long, unbranched pedicel covered with thin perisarc, diameter of pedicel-perisarc not widening from basal to distal. Hydranth size as for most other species of the genus, 30-60 scattered tentacles, 5-7 identical oral tentacles around shallow hypostome. Above and among oral tentacles may be a concentration of macrobasic euryteles.

Gonophores are medusa buds, developing in a cluster in the lower part of the tentacle zone, tentacles not much reduced in medusa-budding hydranths, each bud with a stalk.

Nematocysts: two size-classes of stenoteles; large telotrichous macrobasic euryteles, visible part of shaft in intact macrobasic eurytele of polyp in more than one coil, coiling somewhat variable but typically in the form of an ampersand (&) (see Figs 80C and 81A-H).

Newly liberated medusa almost spherical, on exumbrella four perradial, oval nematocyst patches containing stenoteles. Manubrium simple, tubular, spanning about half of the subumbrellar cavity, no gonads visible. Four radial canals, well visible, no linear swellings. Radial canals end in four marginal bulbs, one opposite pair large, the

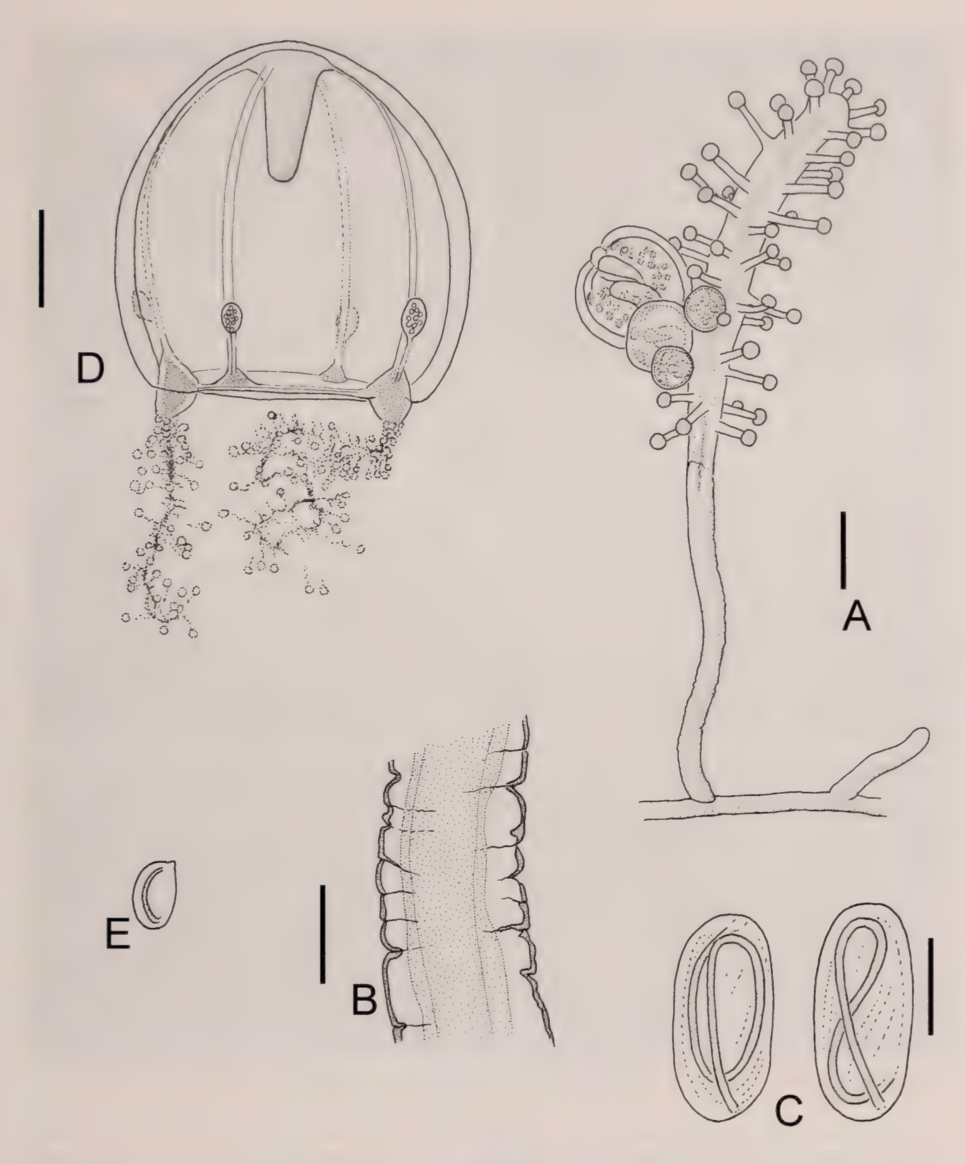


FIG. 80

Zanclea giancarloi Boero, Bouillon, & Gravili, 2000; after living, cultivated material from the Mediterranean. (A) Polyp with medusa buds, note long pedicel of hydranth; scale bar 0.2 mm. (B) Part of pedicel with wrinkled perisarc, scale bar 0.1 mm. (C) Two intact macrobasic euryteles, note variability of shaft coiling, the right capsule shows the typical &-shape of the shaft; scale bar 10 μm. (D) Newly liberated medusa; scale bar 0.2 mm. (E) Intact macrobasic eurytele of the tentacle-nematophores of the medusa; same scale as C.

other very small, large bulbs bearing long, tapering, contractile tentacles with cnidophores, cnidophores all on one side of tentacles, contractile, each with usually 3-5 macrobasic euryteles, distally with long cilia.



FIG. 81

Zanclea giancarloi Boero, Bouillon, & Gravili, 2000; A-H preserved material from La Ciotat, I-K living medusa. (A-H) Macrobasic euryteles of polyp, the pairs E-F and G-H depict the same capsule, but in different focusing planes; scale bar 10 μm. (I) Stenotele of exumbrellar patch; scale bar 10 μm. (J) Macrobasic eurytele of tentacular nematophores; same scale as I. (K) Tentacular nematophores of medusa, scale bar 20 μm.

Mature medusa according to Boero *et al.* (2000), short-lived (matures within 5 days), not much different from young one, tentacles and manubrium longer, gonads interradial, females with two eggs per quadrant.

Nematocysts of medusa: two size-classes of stenoteles; telotrichous macrobasic euryteles in cnidophores; very rare microbasic euryteles may be on exumbrella.

DIMENSIONS: Hydranth 1-2 mm, pedicel 1 mm. Nematocysts of polyp (living specimens): larger stenoteles (12-14)x(12-12.5)μm; smaller stenoteles (7-9)x(6-7)μm; macrobasic euryteles (16-22)x(9-10)μm. Newly liberated and mature medusa 0.5-0.7 mm high. Nematocysts of living medusa: stenoteles about 17μm long; macrobasic euryteles (7-7.5)x(4-5)μm.

OTHER DATA: Can be cultivated relatively easily, but medusa budding can be difficult to induce.

BIOLOGY: The polyps have been found in depths from nearly the water surface to maximal 8 metres, active at least from May to September.

DISTRIBUTION: Mediterranean to Bay of Biscay (Gravili *et al.*, 1996; this study). Type locality: Ionian Sea, Italy, Porto Cesareo.

REMARKS: Boero *et al.* (2000) found two slightly different types of macrobasic euryteles, differing mainly in their size and the length of the spine armature of the shaft. Only one type was found in the material examined for this study.

To me, the polyps of *Z. implexa* and *Z. giancarloi* appear indistinguishable and here they were separated based on their geographic distribution. Their medusae could, however, differ significantly and as long as the adult medusa of *Z. implexa* remains unknown, the two names cannot be synonymized.

Genus ***Halocoryne*** Hadzi, 1917

Halocoryne Hadzi, 1917a; type species *Halocoryne epizoica* Hadzi, 1917a by monotypy.

DIAGNOSIS: Hydroids stolonal, always living in close association with bryozoans; polymorphic; gastrozooids reduced, without tentacles, with or without nematocyst knobs; dactylo-gonozooids rod-shaped, slender, usually with one or two terminal nematocyst knobs, sometimes with lateral rows of nematocyst knobs as well, without mouth. Reproduction by medusoids or tentaculate medusae as given in the family diagnosis. Medusoids without tentacles, without mouth, with four radial canals, four perradial bulbs with nematocyst patch at the abaxial side.

REMARKS: There is only one described species occurring in the ERMS zone. Another species (polyps resembling *H. pirainoid* Boero *et al.*, 2000) occurring on *Schizomavella* spec. was observed in the western Mediterranean (own unpublished observations).

Halocoryne epizoica Hadzi, 1917 — Fig. 82

Halocoryne epizoica Hadzi, 1917a: 1, figs 1-9. – Hadzi, 1917b: 27. – Picard, 1957: 4. – Brinckmann-Voss, 1970: 84, fig. 99. – Bouillon, 1974a: fig. 14. – Petersen, 1990: 205, fig. 41. – Piraino & Boero, 1992: 143, figs 1-3. – Boero *et al.*, 2000: 111, fig. 15. – Bouillon *et al.*, 2004: 112, fig. 58D-E.

MATERIAL EXAMINED: ZMUC, without registration number; Mediterranean, Ligurian Sea, France, Tamaris; collected June 1971 by J. Bouillon; large, fertile colony on *Schizobrachiella sanguinea*.

DIAGNOSIS: *Halocoryne* growing on bryozoan *Schizoporella sanguinea*, dimorphic polyps without tentacles, releasing mouthless medusoids without tentacles.

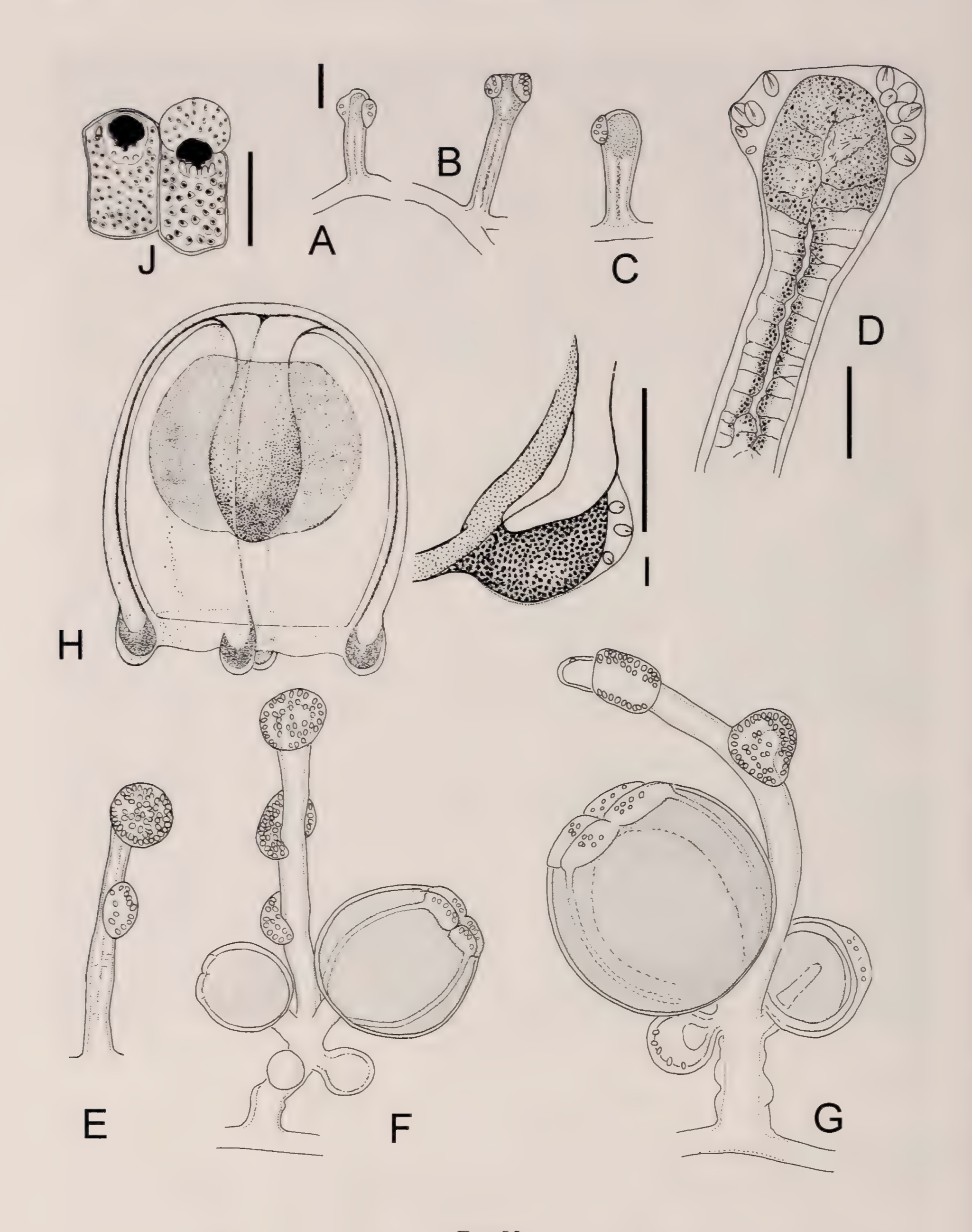


FIG. 82

Halocoryne epizoica Hadzi, 1917; A-G drawn after preserved material, H from Bouillon (1974a), I from Piraino & Boero (1992), J from Zabala & Maluquer (1988). (A-C) Gastrozooids arising from stolons; scale bar 0.2 mm. (D) Distal end of gastrozooid in optical section; scale bar 50 μm. (E) Young dactylo-gonozooid before gonophore development, same scale as A. (F-G) Dactylo-gonozooids with medusa-buds, same scale as A. (H) Liberated medusoid, size about 1 mm. (I) Marginal bulb of medusoid in side view, note abaxial nematocyst patch, scale bar 0.1 mm. (J) Two *Schizoporella sanguinea* zooids (skeleton), right one with ooecium, scale bar 1 mm.

DESCRIPTION: Colonies growing on *Schizoporella sanguinea*. Hydranths issued from a reticulated stolon system following the borders of the host zooids, stolons without discernible perisarc, normally covered by the bryozoan skeleton but often uncovered near the periphery of the host colony. Hydranths relatively small and inconspicuous, usually near the orifice of the host, without distinct pedicel, dimorphic with gastrozooids and dactylo-gonozooids, both types very contractile.

Gastrozooids rod-shaped, thin and small, without tentacles, usually with two subterminal nematocyst knobs below the hypostome, the two nematocyst buttons may be fused partially, or connected by smaller clusters, or only one button is present.

Dactylo-gonozooids rod-shaped, with a terminal or subterminal knob of nematocysts and up to five more proximal nematocyst clusters on one side. When carrying medusa buds, dactylo-gonozooids slightly shorter but much thicker and not as contractile as the other polyps, with a terminal knob of nematocysts continuing proximally toward the base in an irregular and interrupted spiral of tightly packed nematocysts. Medusa buds near the base of the polyp, up to four in different stages of development.

Gonozooids dark red, other polyps dark red to transparent.

Nematocysts: stenoteles of two sizes.

Gonophores are non-feeding, short-lived medusoids which may be liberated or not (Piraino & Boero, 1992). Liberated medusoids bell-shaped, four radial canals connecting the base of the manubrium with four atentaculate triangular bulbs at bell margin, connected by ring canal, bulbs with nematocyst patch at the abaxial side. Manubrium length reaching two thirds the height of subumbrellar cavity, completely encircled by gonad, without mouth. Manubrium, bulbs, radial canals and circular canal all dark red due to dense granules identical to those of the dactylo-gonozooids. Exumbrella armed with small macrobasic mastigophores (can be confounded with desmonemes). Nematocysts of bulbs stenoteles of two sizes and very rare (0-3 per medusa) tentatively identified macrobasic euryteles.

DIMENSIONS: Contracted polyps just less than 0.2 mm, fully extended specimens reaching almost 1.5 mm. Free medusoids about 1 mm.

BIOLOGY: *Halocoryne epizoica* occurs only on the orange to purple encrusting bryozoan *Schizobrachiella sanguinea* (Norman). The cheilostomate bryozoan *Schizobrachiella sanguinea* has a wide distribution in the Mediterranean Sea and is a frequent coloniser of a wide range of sublittoral, often sciaphilic, habitats between 10 and 50 m (Mariani *et al.*, 2005). The gastrozooids of *H. epizoica* feed on the lophophore-tentacles of their bryozoan host (Piraino & Boero, 1992). They are able to ingest and remove a single tentacle-tip, but seem not to be too much of a nuisance to their host. *Halocoryne epizoica* is a common species along the Apulian coast, occurring on almost all colonies of *Schizobrachiella sanguinea* (Piraino & Boero, 1992). Reproductive colonies were found in June-July. The gametes may be released while the medusoid is still attached to the hydroid, liberated medusoids die after a few hours of active swimming.

DISTRIBUTION: Endemic to the Mediterranean (Piraino & Boero, 1992). Type locality: Trieste, Adriatic Sea, on *Schizobrachiella sanguinea* collected in 103 m depth.

FAMILY CORYNIDAE JOHNSTON, 1836 (sensu Nawrocki *et al.*, 2010)

Corynidae Johnston, 1836.
Sarsiadae Forbes, 1848.
Syncorynidae Allman, 1872.
Codonidae Haeckel, 1879.
Polyorchidae A. Agassiz, 1862.

DIAGNOSIS: The least inclusive clade comprising the species *Coryne pusilla* Gaertner, 1774; *Stauridiosarsia producta* (Wright, 1858); and *Sarsia tubulosa* (M. Sars, 1835).

REMARKS: All species of the family Corynidae have been reviewed in Schuchert (2001b) and they need not be treated in detail again here. However, the phylogenetic analysis of Nawrocki *et al.* (2010) has shown that the scope of the family and most of its genera must be revised. At the family level, the most important finding was that the Polyorchidae are actually part of the Corynidae clade. This somewhat surprising result makes it nearly impossible to provide a useful and concise morphological diagnosis of the Corynidae. We have to resort to a phylogenetic diagnosis as given above, which, in practice, should not pose too much of a problem. More difficult to accept are the new genus delimitations resulting from the molecular phylogeny. The Corynidae must be subdivided at least into the following genera: *Coryne*, *Codonium*, *Slabberia* (syn. *Dipurena*), *Sarsia*, *Stauridiosarsia*, *Scrippsia*, and *Polyorchis*. While some genera like *Sarsia* and to a lesser extent *Coryne* retain their traditional scope, *Slabberia* (*Dipurena*) changes completely and *Stauridiosarsia* and *Codonium* have to be reintroduced. Some genera now have the disadvantage of being utterly uninformative and their diagnosis must rely on phylogenetic definitions. Another major disadvantage of this new system is that species which were not included in the analysis of Nawrocki *et al.* cannot be classified reliably and have to be placed in the genus *Coryne* by default. Despite these shortcomings, the new classification should be adopted nevertheless. The subdivision of the Corynidae has changed many times during the last decades and most groupings are obviously polyphyletic and unnatural. The system of Nawrocki *et al.* is based on well founded clades and thus provides the much needed framework for a classification that will remain ultimately stable.

KEY TO SPECIES OF CORYNIDAE OF THE ERMS ZONE:
(only species for which the mature medusa or the sporosacs are known)

1a gonophores are sporosacs or medusoids lacking tentacles or having only rudimentary tentacles 2
1b life cycle includes a medusa with four tentacles, adult morphology is known 9
2a gonophores are sporosacs 3
2b gonophores oblong medusoids with no or only rudimentary tentacles . . . . *Sarsia lovenii*
3a polyps on small gastropod shells living in Mediterranean sea grass beds . . . . *Coryne epizoica*
3b polyps living on other substrates 4
4a sporosacs in axils of the capitate tentacles 5

4b sporosacs independent of tentacles, with four radial canals . . . *Coryne hincksii*
5a viviparous, young polyps develop in sporosacs . . . . *Coryne vanbenedenii*
5b oviparous, eggs are spawned into the water and develop into planulae 6
6a polyp has scattered capitate tentacles and a basal whorl of filiform tentacles (may be visible in culture only) . . . . *Coryne pintneri*
6b polyps never with filiform tentacles 7
7a polyp thin, elongate, worm-like, 2-7 mm . . . . *Coryne fucicola*
7b polyps more club-shaped, usually less than 2.5 mm 8
8a colonies elongate, with long main axis and shorter side branches, completely annulated, base of polyp often in perisarc cup [in Mediterranean often not distinguishable from *C. pusilla*] . . . . *Coryne muscoides*
8b colonies bushy, broad, stem perisarc annulated and smooth [absent Mediterranean] . . . . *Coryne pusilla*
9a medusa with manubrium shorter or as long as height of subumbrellar cavity 10
9b medusa with manubrium much longer than bell height 12
10a medusa with medusa buds on marginal bulbs . . . . *Codonium proliferum*
10b medusa without medusa buds on bulbs 11
11a colonies branched, polyps without filiform tentacles; medusa without apical canal . . . . *Coryne eximia*
11b colonies stolonal, polyps with filiform tentacles; medusa with apical canal . . . . *Stauridiosarsia producta*
12a medusa with medusa buds on manubrium . . . . *Stauridiosarsia gemmifera*
12b medusa without medusa buds on manubrium 13
13a medusa tentacles with a large terminal nematocyst cluster, with or without some subterminal clusters, more than half of the tentacle free of nematocyst clusters; polyps exclusively on sponges 14
13b medusa with many nematocyst clusters on tentacles, covering more than half of the tentacle 15
14a several nematocyst clusters in terminal tentacle region, apical chamber above manubrium, usually two gonad rings; polyp base enveloped in persisarc . . . . *Slabberia halterata*
14b a single terminal nematocyst cluster, no apical chamber above manubrium, usually only one gonad on manubrium; polyp base not enveloped in perisarc . . . . *Slabberia simulans*
15a gonads covering also stomach portion at end of long manubrium, gonad split into 2 or more rings 16
15b gonads not extending onto stomach portion at end of long manubrium, gonad undivided 17
16a usually 2 gonad rings; polyp with 4-5 capitate tentacles in one oral whorl . . . . *Stauridiosarsia reesi*
16b 3-9 gonad rings; polyps with 10-18 scattered capitate tentacles . . . . *Stauridiosarsia ophiogaster*
17a in Arctic, bell > 12 mm, subumbrella pointed, thin apical canal above manubrium . . . . *Sarsia princeps*

17b bell usually <12 mm, subumbrella rounded, apical chamber instead of apical canal 18
18a medusa with angular subumbrellar pockets at apex; polyp with filiform tentacles . . . . *Sarsia striata*
18b without angular subumbrellar pockets; polyp with or without filiform tentacles 19
19a gonad free portion of manubrium shorter than subumbrellar height; polyp colonies stolonal or sparingly branched 20
19b gonad free portion of manubrium longer than subumbrellar height; polyp colonies much branched . . . . *Sarsia densa*
20a polyp with more than one whorl of capitate tentacles; top of medusa bell rounded 21
20b polyp with one whorl of capitate tentacles and one whorl of filiform tentacles; apical jelly of medusa thick and shape conical . . . . *Sarsia piriforma*
21a medusa max. 3.4 mm, gonad develops while medusa is still attached to polyp . . . . *Sarsia occulta*
21b young medusa released without visible gonads, adult medusa 4-10 mm in height . . . . *Sarsia tubulosa*

Genus ***Coryne*** Gaertner, 1774 [sensu Nawrocki *et al*., 2010]

Coryne Gaertner, 1774; type species *Coryne pusilla* Gaertner, 1774 by monotypy.
Fistularia Müller, 1776, invalid junior homonym of *Fistularia* Linnaeus, 1758 [Pisces].
Fistulana Müller, 1776; no type species designated.
Capsularia Modeer, 1793. [nomen nudum]
Capsularia Cuvier, 1798.
Corine Cuivier, 1798. [incorrect spelling]
Coryna Bosc, 1802. [incorrect spelling]
Corina Schweigger, 1820. [incorrect spelling]
Stipula M. Sars, 1829; type species *Stipula ramosa* Sars, 1829 by monotypy.
Syncoryna Ehrenberg, 1834; no type species designated.
Hermia Johnston, 1838a; type species *Hermia glandulosa* Brugière, 1789 by monotypy (Johnston, 1838b: 111).
Syncoryne Steenstrup, 1842. [incorrect spelling]
Halybotrys de Filippi, 1866; type species *Halybotrys fucicola* de Filippi, 1866 by monotypy.
? *Actinogonium* Allman, 1872; invalid junior homonym of *Actinogonium* Schomburgk [Protozoa].
Halobotrys Carus, 1885. [incorrect spelling]
Syncorine Spagnoli, 1871. [incorrect spelling]
Staurocoryne Rotch, 1872; type species *Staurocoryne wortleyi* Rotch, 1872.
Eucoryne Broch, 1910; invalid junior homonym of *Eucoryne* Leidy, 1855 (Hydrozoa).
Halybothrys Bedot, 1910. [incorrect spelling]
Actigia Stechow, 1921b; for *Syncoryna pusilla* of van Beneden, 1844a [= *Coryne vanbenedenii* Hincks, 1868].

Diagnosis: The least inclusive clade comprising the species *Coryne pusilla* Gaertner, 1774; *C. pintneri* Schneider, 1898; and *C. eximia* Allman, 1859.

Remarks: The scope of this genus is now as proposed in Nawrocki *et al*. (2010). The European fauna comprises the following species: *Coryne epizoica* Stechow, 1921; *C. eximia* Allman, 1859; *C. fucicola* (de Filippi, 1866); *C. hincksii* Bonnevie, 1898; *C. muscoides* (Linnaeus, 1761); *C. pintneri* Schneider, 1898; *C. pusilla* Gaertner, 1774; and *C. vanbenedenii* Hincks, 1868.

Most, but not all, species of this clade have axillar gonophores, which is a synapomorphy. In the European fauna, only *C. hincksii* and perhaps *Coryne vanbenedenii* have sporosacs which do not develop in the axils of the tentacles. The taxonomic position of both species is not well established as they were not included in the molecular phylogeny of Nawrocki *et al.* (2010). *Coryne* can also be used as the default genus for those species for which not enough molecular or morphological data is available to link them confidently to one of the redefined genera.

Nearly all species of this genus have been described and depicted in Schuchert (2001b). Some important updates are, however, necessary.

The gonophores of *Coryne epizoica* have been described in Schuchert & Brinckmann-Voss (2006). What was previously suspected to be the gonophores is in fact an adhesive organ used for colonizing other shells.

The status of *C. pusilla* and *C. muscoides* was examined by Schuchert (2005a) using molecular methods. Atlantic populations of both species are more or less well distinguishable as their variation is low enough to separate them based on colony morphology. In contrast, *Coryne muscoides* of the Mediterranean shows a much higher degree of morphological and genetic variation. The morphological variation also encompasses the morphotype of the Atlantic *C. pusilla*. No unambiguous identifications of Mediterranean *C. pusilla* are known and the species is likely absent from the Mediterranean. Mediterranean records of *C. pusilla* are either referable to *C. muscoides* or *C. pintneri* lacking filiform tentacles. The Atlantic population of *C. muscoides* originated likely through a colonizing event of a small Mediterranean subpopulation. At a global level, *C. pusilla* seems to be a species complex.

The status of *Coryne vermicularis* Hincks, 1866 as a synonym of *C. pusilla* has been confirmed. The nominal species *Coryne vermicularis* was introduced by Hincks (1866) for material from the Shetland Islands which resembled *C. pusilla*, but had much larger hydranths (see also Schuchert, 2005b). *Coryne* colonies with identical morphotypes as *C. vermicularis* were found by myself near Bergen, Norway (MHNG INVE 48737 and 48738). Their partial 16S sequences were identical to sequences of *C. pusilla* from the English Channel and Scotland (Schuchert, 2005b and unpublished data).

Type material of *Coryne filiformis* (Rees, 1936) (BMNH 1985.9.1.9-10; BMNH 1969.12.2.97-98, type locality Plymouth) was examined for this study. Both samples are indistinguishable from cultivated *C. pintneri* from Roscoff (English Channel) and the Mediterranean. Partial 16S sequence data of the Roscoff colony and Mediterranean *C. pintneri* confirmed that they belong to the same clade and likely species (comp. Schuchert, 2005b: fig. 3). Contrary to Edwards & Harvey (1983), *Coryne filiformis* (Rees, 1936) is therefore here regarded as conspecific with *Coryne pintneri* Schneider, 1898.

Coryne fucicola (de Filippi, 1866) is a valid and distinct species, it was redescribed by Schuchert (2005b) based on a colony from the English Channel.

Genus ***Codonium*** Haeckel, 1879 [sensu Nawrocki *et al.*, 2010]
Codonium Haeckel, 1879; type species *Codonium codonoforum* Haeckel, 1879.

Diagnosis: Comprises *Codonium proliferum* (Forbes, 1848) and similar Corynidae with medusae budding from tentacle bulbs.

REMARKS: When establishing the genus *Codonium*, Haeckel (1879) included four species in it: *C. princeps* Haeckel, 1879 [today *Sarsia princeps*], *C. gemmiferum* (Forbes, 1848), *C. codonophorum* [a synonym of *S. proliferum*], and *C. pulchellum* (Forbes, 1848) [a synonym of *S. tubulosa*]. Haeckel created the genus for species with a thickened apical jelly containing an apical canal, but he did not designate a type species. Browne (1903) then synonymized the genus *Codonium* with *Sarsia* Lesson, 1843. This was also accepted by subsequent influential revisers like Hartlaub (1907) and Mayer (1910) and the genus was not used anymore. To my knowledge, no type species has ever been designated. Nawrocki *et al.* (2010) suggested that *C. codonophorum* Haeckel, 1879 should be designated as type species of the species in order to make it available specifically for *C. proliferum*. This suggestion, made in an electronic appendix, does not meet the requirements of the ICZN. Therefore, *Codonium codonophorum* Haeckel, 1879 is herewith selected as type species of the genus *Codonium* Haeckel, 1879. *Codonium codonophorum* Haeckel, 1879 has been treated as a questionable synonym of *C. prolifera* (Mayer, 1910; Brinckmann-Voss, 1970; Schuchert, 2001b), differing only in its larger size, the presence of an apical canal, and its occurrence in the Mediterranean. Such a canal or chamber is also occasionally present in Atlantic *C. proliferum* (see Russell, 1953) and both nominal species can be safely regarded as conspecific. The genus thus presently contains only *Codonium proliferum* (Forbes, 1848) (formerly *Sarsia* or *Coryne prolifera*). The genus change also requires changing the specific epithet from prolifera to proliferum as the gender of the Greek word *Codonium* [κουδούνι] is neuter. *Codonium* is also an accepted plant genus.

The molecular phylogeny of Nawrocki *et al.* (2010) placed *C. proliferum* quite apart from the other genera used here. This, together with the rather unique and apomorphic trait "medusa-budding from the tentacle bulbs", justifies the creation of a monotypic genus.

Genus ***Slabberia*** Forbes, 1846 [sensu Nawrocki *et al.*, 2010]

not *Slabberia* Oken, 1815: 828, invalid name published in a work rejected for nomenclatural purposes by the ICZN, Opinion 417.

Slabberia Forbes, 1846: 286; type species *Slabberia halterat*a Forbes, 1846 by monotypy.

Systrepha Gistl, 1848: 381, new name for *Slabberia* Forbes, 1846.

Dipurena McCrady, 1859: 135; type species *Dipurena strangulata* McCrady, 1859 (Kramp, 1961).

DIAGNOSIS: The least inclusive clade comprising the species *Slabberia halterata* Forbes, 1846 and *Slabberia simulans* (Bouillon, 1965).

REMARKS: The genus name *Slabberia* Forbes, 1846 was widely used until Mayer (1910: 719) noted that the name is a junior homonym of *Slabberia* Oken, 1815. Oken's work was, however, rejected for nomenclatural purposes (ICZN, 1956: opinion 417). This makes *Slabberia* Forbes, 1846 a valid name again. *Slabberia* and *Dipurena* McCrady, 1859 have unanimously been regarded as synonyms by most taxonomists of the later 20th century. Because Forbes' name is older, *Slabberia* must be used. At first it might appear somewhat inconvenient that the now well known name *Dipurena* should be replaced by the less known *Slabberia*. However, the work of Nawrocki *et al.*

(2010) has shown, that the traditional scope of *Dipurena*, as defined by their subdivision of the gonad, cannot be upheld and the genus is clearly polyphyletic. Unaware of the taxonomic problem relating to *Slabberia*, Nawrocki *et al.* suggested restricting the scope of *Dipurena* to a clade comprising the three species given in the diagnosis above. *Dipurena* gets thus a rather different meaning from the one of previous authors and it is actually advantageous if also a less-used name is used for this clade. Furthermore, the analysis of Nawrocki *et al.* did not include the type species of *Dipurena* (*D. strangulata*), but it included the type species of *Slabberia*, *S. halterata*. The genus *Slabberia* is thus better defined at a molecular level.

Dipurena strangulata, *S. halterata*, and *S. simulans* resemble each other closely and likely belong to the same clade (genus). The polyps occur exclusively on sponges only and the medusae have a large terminal nematocyst cluster, with or without some subterminal clusters, more than half of the proximal part of the tentacles remains free of nematocyst clusters. *Stauridiosarsia marii* is somewhat similar, but its polyps do not occur on sponges.

The European fauna comprises *Slabberia halterata* Forbes, 1846 and *Slabberia simulans* (Bouillon, 1965).

Genus ***Sarsia*** Lesson, 1843 [sensu Nawrocki *et al.*, 2010]

Sarsia Lesson, 1843; type species *Oceania tubulosa* M. Sars, 1835 by monotypy.
Sthenyo Dujardin, 1845; type species by monotypy is *Syncoryne decipiens* Dujardin, 1845: 275, pl. 14-15, medusa named *Sthenyo*, synonym of *Sarsia tubulosa* (M. Sars, 1835).
Syndiction A. Agassiz, 1862; no type species specified.

Diagnosis: The least inclusive clade comprising the species *Sarsia tubulosa* (M. Sars, 1835); *S. lovenii* (M. Sars, 1846); and *S. apicula* (Murbach & Shearer, 1902).

Remarks: The genus *Sarsia* sensu Petersen, 1990 was the only Corynidae genus retrieved as monophyletic by the molecular phylogeny of Nawrocki *et al.* (2010). The morphological diagnosis given in Schuchert (2001b) thus remains valid.

The following species occur within the ERMS zone: *Sarsia tubulosa* (M. Sars, 1835); *Sarsia densa* (Hartlaub, 1897); *Sarsia lovenii* (M. Sars, 1846); *Sarsia occulta* Edwards, 1978; *Sarsia piriforma* Edwards, 1983; *Sarsia princeps* (Haeckel, 1879); and *Sarsia striata* Edwards, 1983. *Sarsia densa* is somewhat dubious; it is perhaps conspecific with *S. tubulosa*.

Genus ***Stauridiosarsia*** Mayer, 1910 [sensu Nawrocki *et al.*, 2010]

Stauridiosarsia Mayer, 1910 (subgenus of *Sarsia*); type species *Stauridia producta* Wright, 1858 by monotypy.
Perinema Stechow, 1921a; type species *Coryne cerberus* Gosse, 1853 by original designation [synonym of *Stauridiosarsia producta* (Wright, 1858)].

Diagnosis: The least inclusive clade comprising the species *Stauridiosarsia producta* (Wright, 1858); *St. ophiogaster* Haeckel, 1879; and *St. gemmifera* (Forbes, 1848).

Remarks: The molecular phylogeny of Nawrocki *et al.* (2010) united *St. producta* (Wright, 1858) together with species hitherto placed in *Coryne* and *Dipurena*. All examined species of this clade produce medusae, but some have a short manubrium

like *St. producta*, *St. cliffordi*, and *St. nipponica*, others have a long manubrium with split gonads typical of *Dipurena* medusae in the sense of Petersen (1990). The support for this rather unexpected clade was robust and it is advisable to use it, despite the impossibility of giving a usable morphology-based diagnosis.

The following species of the ERMS zone belong to this genus: *St. producta* (Wright, 1858); *St. ophiogaster* (Haeckel, 1879); *St. gemmifera* (Forbes, 1848); and *St. reesi* (Vannucci, 1956). *Sarsia marii* Schierwater & Ender, 2000 and *Dipurena spongicola* Anger, 1972 are both insufficiently known and should be placed provisionally in the genus *Stauridiosarsia*. The 16S data associated *St. marii* with this clade, but without reliable support for the nodes.

CAPITATA INCERTA SEDIS

Genus ***Plotocnide*** Wagner, 1885

Plankayon Wagner, 1880; *nomen nudum*.
Plotocnide Wagner, 1885; type species *Plotocnide borealis* Wagner, 1885 by monotypy.

DIAGNOSIS: Medusa umbrella evenly rounded with thick apical jelly and scattered groups of exumbrellar nematocysts; manubrium half as long as bell cavity, with or without broad, dome-shaped apical chamber; mouth simple, with ring of nematocysts; gonad forming thick ring around manubrium; four narrow radial canals and narrow ring canal; four marginal bulbs each with a solid tentacle terminating in ovoid knob studded with nematocysts. No ocelli. Cnidome comprises stenoteles and desmonemes. Polyps unknown.

Plotocnide borealis Wagner, 1885 — Fig. 83

? *Plankayon hyalinus* Wagner, 1880: 195, *nomen nudum*.
Plotocnide borealis Wagner, 1885: 74, pl. 4 figs 1-2. – Hartlaub, 1907: 69, figs 65. – Kramp, 1942: 22, figs 5-6. – Beyer, 1955: 94, fig. 1. – Kramp, 1959: 91, fig. 45. – Kramp, 1961: 45. – Kramp, 1968: 17, fig. 37. – Naumov, 1969: 240, fig. 110. – Russell, 1970: 233. – Arai & Brinckmann-Voss, 1980: 12, fig. 5.
Protiara borealis. – Mayer, 1910: 106.
Sarsia inabai Uchida, 1933: 126, fig. 2. – Uchida, 1969: 286, synonym.
Eucodonium arctica Hand & Kan, 1961: 9, fig. 5. – Arai & Brinckmann-Voss, 1980: 12, synonym.
not *Sarsia inabai*. – Bouillon, 1978a: 131, fig. 3. – Bouillon, 1985b: 248, fig. 1. [= new species]
? not *Plotocnide borealis*. – Goy *et al.*, 1991: 105, fig. 11.
not *Coryne inabai*. – Schuchert, 2001b: 770, fig. 11B. [= new species]

MATERIAL EXAMINED: ZMUC, without registration number; Greenland, Skinderhvalen, 63.733°N 51.583°W; 1 damaged medusa collected 14.07.1934; det. P. Kramp.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION (Kramp, 1959; Arai & Brinckmann-Voss, 1980; own observations): Medusa umbrella hemispherical to bell-shaped, usually almost as wide as high, apex rather thick, rounded, apical jelly may have a thickness of up to one third the height of the medusa, exumbrella with loose groups of stenoteles. Manubrium about half as long as bell cavity, simple, often with gastrodermal oil-droplets that bulge into apical mesogloea like a broad apical chamber, mouth simple with a ring of nematocysts; gonads ringlike, encircling stomach completely, thick and bulging, leaving only lips and uppermost portion of manubrium free, females with numerous eggs. Four

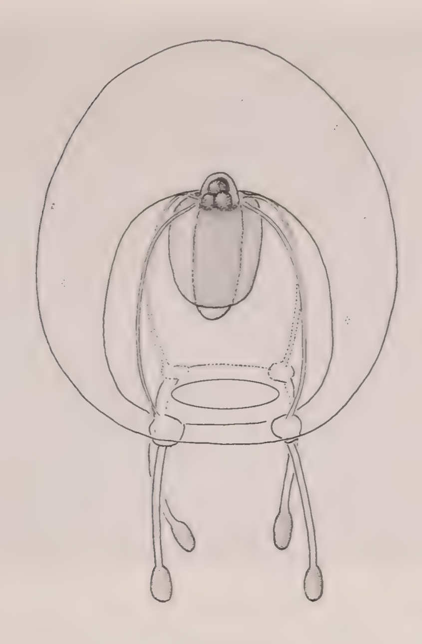


FIG. 83
Plotocnide borealis Wagner, 1885; bell size about 2 mm; combined after several sources.

straight, narrow radial-canals and thin circular canal, radial canals ending in moderately sized marginal bulbs, ocelli absent but some specimens with small gastrodermal pigment masses in tentacle bulbs. Four perradial tentacles, length variable, contractile, up to twice as long as the height of the bell, each ending in an oblong nematocyst-bearing knob, rest of tentacles with few nematocysts. Colour of terminal tentacle knobs and tip of manubrium reddish in living specimens.

Nematocysts (Hand & Kan, 1961): desmonemes and stenoteles.

Polyp stage unknown.

DIMENSIONS: Bell height when mature 1.5-3.5 mm. For nematocyst measurements see Hand & Kan (1961).

VARIATION: Beyer (1955) observed a medusa with six tentacles, two bulbs bearing a pair of tentacles. It is possible that animals with eight tentacles (two per bulb) exist.

BIOLOGY: Occurs in depths of 0-200 m (Naumov, 1969). In the Arctic Sea, this seems to be a common species present in the plankton all year, decreasing in numbers in November-January and reaching its maximum in April-June, when juveniles are also encountered (Zelickman, 1972).

DISTRIBUTION: Arctic circumpolar and northern boreal species, in Europe reaching as far south as the Clyde Sea (Scotland: Edwards, 1958) and Oslofjord (Norway: Beyer, 1955), in the western Atlantic south to Davis Street, in the Pacific south to Kamchatka and Vancouver Island, (Kramp, 1942, 1968; Naumov, 1969;

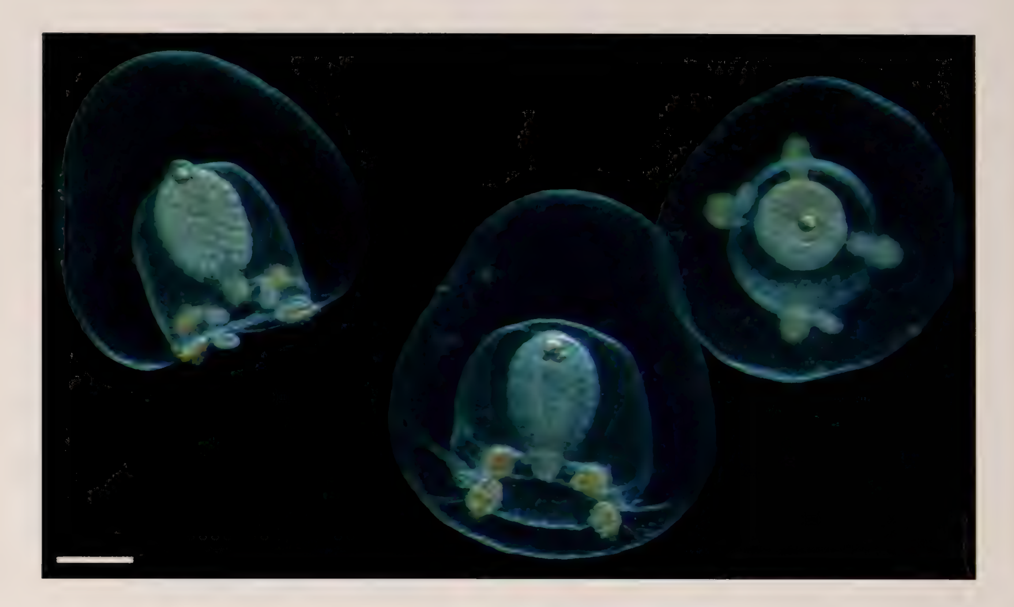


FIG. 84

Plotocnide borealis Wagner, 1885; living female medusae, tentacles mostly lost, scale bar 0.5 mm. The photo was kindly provided by Dr. Russell R. Hopcroft, Institute of Marine Science, University of Alaska at Fairbanks.

Zelickman, 1972; Arai & Brinckmann-Voss, 1980). The Mediterranean record of Goy *et al.* (1991) is almost certainly based on a misidentification (Bouillon *et al.*, 2004). Type locality: White Sea, Solovetsky Islands.

Genus ***Rhabdoon*** Keferstein & Ehlers, 1861

Rhabdoon Keferstein & Ehlers, 1861; type species *Rhabdoon singulare* Keferstein & Ehlers, 1861 by monotypy.

Rhysomedusa Vanucci & Soares Moreira, 1966; type species *Rhysomedusa pomponina* Vannucci & Soares Moreria, 1966 by monotypy.

Pararhysomedusa Shirley & Leung, 1970; type species *Pararhysomedusa reesi* Shirley & Leung, 1970 by monotypy.

Yakovia Margulis, 1989; type species *Yakovia polinae* Margulis, 1989 by original designation.

Eugotoea Margulis, 1989; type species *Eugotoea petalina* Margulis, 1989 by original designation.

DIAGNOSIS: Medusa with a single hollow tentacle ending in a sphere of radiating nematophores; exumbrella with meridional nematocyst bands; vacuolated cells at apex of manubrium, along radial canals, and around the umbrella margin; four radial canals; marginal bulbs absent or only one present where tentacle is attached; manubrium simple, not or not much longer than subumbrellar height, gonads surround manubrium completely; cnidome includes stenoteles, desmonemes, and microbasic heteronemes.

REMARKS: See Stepanjants & Kosobokova (2006) for a recent revision of this genus. The polyp stage of *Rhabdoon* remains unknown, therefore it is also not clear whether this genus belongs to the Tubulariidae or the Corymorphidae. Therefore it was classified here as *incerta sedis*. Stepanjants & Kosobokova (2006) noted an interesting

similarity of the cnidophores at the tentacle tip in *Rhabdoon* and *Euphysa furcata* (see Schuchert, 1996 for a redescription).

IDENTIFICATION KEY OF *RHABDOON* SPECIES

1a marginal bulbs absent . . . . *R. singulare*
1b with one marginal bulb bearing the single tentacle . . . . *R. reesi*

Rhabdoon singulare Keferstein & Ehlers, 1861 Fig. 85

Rhabdoon singulare Keferstein & Ehlers, 1861:86, pl. 13 figs 6-7. – Pagès *et al.*, 1992: 21, fig. 20. – Bouillon *et al.*, 2004: 108, fig. 56J. – Stepanjants & Kosobokova, 2006: 394.
Rhysomedusa pomponina Vannucci & Soares Moreria, 1966: 8, fig. 1-8. – Brinckmann-Voss, 1970: 32, fig. 35. – Goy, 1973: 973, fig. 4a-b. – Hamond, 1974: 552, fig. 1-2. – Brinckmann-Voss, 1987: 135, synonym.
Eugotoea petalina Margulis, 1989: 129, fig. 2Ж-И. **new syn**.
Eugotoea petalina. – Bouillon *et al.*, 2004: 92, fig. 49D-F.

MATERIAL EXAMINED: BMNH 1985.3.20.1, as *Rhysomedusa pomponina*; east of Gibraltar, 35.823°N 04.75°W, 0-200 m; 1 medusa collected 25.10.1981. – MNHN 1621; Mediterranean, France, Villefranche-sur-mer, 0-150 m; 3 fertile medusae; material of Goy (1973).

DIAGNOSIS: *Rhabdoon* species without marginal bulb.

DESCRIPTION (after own data and various literature sources): Medusa umbrella ellipsoid to spherical, rounded top, bell margin oblique, longest perradial side is tentacular one, jelly moderately thick, not much thickened at apex. Exumbrella with four exerted, perradial ribs running meridionally from margin to near top, dark, containing refractile droplets and nematocysts, in middle of each perradial rib an oblong inclusion which makes rib bulge, this inclusion composed of denser material, white in preserved animals, brown in living ones. More shallower and shorter exumbrellar ribs can be found in adradial and interradial position, resembling more exumbrellar bands, number and length variable, likely age-related. The darker tissue of the exumbrellar ribs and tracks unite at the bell margin to form a massive nematocyst ring. Manubrium simple, conical, reaching to velum level, attached to a broad gastric peduncle with large vacuolated cells. Gonad encircles manubrium entirely, may fill entire subumbrella. Four radial canals, difficult to observe, no distinct margin bulbs, no ocelli. A single, rather short tentacle (shorter than bell size), composed of a thin proximal part and a large spherical end, terminal knob resembling pompon, composed of radially arranged nematophores.

Cnidome comprises stenoteles (Hamond, 1974).

DIMENSIONS: Bell height 0.7-2.1 mm. Some nematocyst measurements are given in Hamond (1974).

BIOLOGY: A rare medusa, so far found in the depth range 0-220 m. In the western Mediterranean, the medusa has been found in the plankton from January to September (Goy, 1973; Brinkmann-Voss, 1987).

DISTRIBUTION: Mediterranean Sea (Vanucci & Soares Moreira 1966; Brinckmann-Voss 1970; Goy, 1973; 1983; Benovic & Lucic, 1996), south-eastern Atlantic (Pagès *et al.*, 1992), Magellan Straits (Pagès & Orejas, 1999), off Western Australia (Hamond, 1974). Type locality: Messina, Italy.

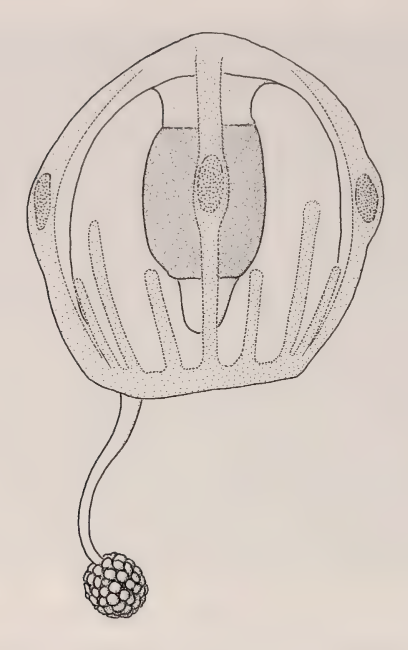


FIG. 85
Rhabdoon singulare Keferstein & Ehlers, 1861; schematic after preserved material, bell size 1.1 mm.

REMARKS: *Eugotoea petalina* Margulis, 1989, known from three specimens collected in the Mediterranean, is characterized by its lack of marginal bulbs, four pigment spots on the exumbrella, and broad, sharply demarcated interradial furrows of the exumbrella. The furrows let the perradial slices of the exumbrella stand out like petals of a flower. In the same paper (Margulis, 1989) also described another species with similar meridional ribs: *Paragotoea elegans*. Pagès & Bouillon (1997) found that these ribs are only preservation artefacts. These ribs are folds linked to the contraction of the mesogloea due to preservation. Although *Rhabdoon singulare* seems to possess ribs when alive, fixation and shrinkage caused by the collection stress must have likely produced the pronounced ribs observed in Margulis' medusae. Animals with similar, though less broad, ribs were also depicted by other authors (e. g. Keferstein & Ehlers, 1861: pl. 13; figure 6; Goy, 1973: Fig 4B; Hamond, 1974: figs 1-2). *Eugotoea petalina* is thus here regarded as a new synonym of *Rhabdoon singulare*.

Rhabdoon reesi (Shirley & Leung, 1970) Fig. 86

Pararhysomedusa reesi Shirley & Leung, 1970: 4, fig. 6.
Yakovia polinae Margulis, 1989: 126, fig. 1. – Stepanjants & Kosobokova, 2006: 393, synonym
Rhabdoon reesi. – Stepanjants & Kosobokova, 2006: 393, figs 2A-F, 3A-D, 4, 5A-D.

DIAGNOSIS: *Rhabdoon* species with a single marginal bulb.

DESCRIPTION (Stepanjants & Kosobokova, 2006): Medusa umbrella bell-shaped, flat top, bell margin oblique, longest perradial side is tentacular one, jelly moderately thick, not much thickened at apex. Exumbrella with four perradial ribs

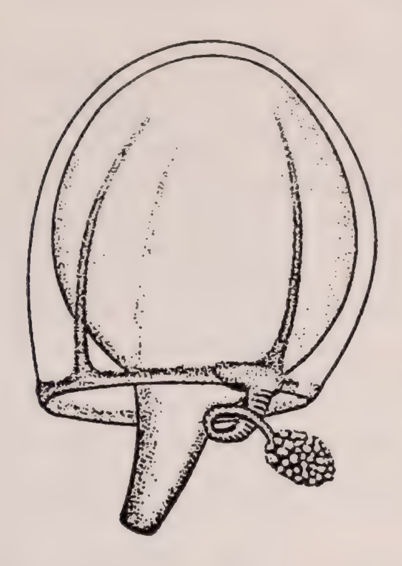


FIG. 86
Rhabdoon reesi (Shirley & Leung, 1970); from Shirley & Leung (1970).

running meridionally from margin to near top; umbrella walls and ribs contain vacuolated cells. Flask-shaped manubrium with a simple round opening, situated on a tubular neck, manubrium extending slightly beyond the velar opening. Three marginal bulbs rudimentary, the fourth bearing the tentacle is well-developed. A single, rather short tentacle (shorter or as long as bell size), composed of a thin proximal part and a large spherical end, terminal knob resembling pompon, composed of radially arranged nematophores.

Nematocysts: stenoteles of three size classes, desmonemes, and microbasic heteronemes.

DIMENSIONS: Bell height 1 to 5 mm, maximum diameter 3.3 mm. For more details, including nematocyst measurements see Stepanjants & Kosobokova (2006).

DISTRIBUTION: Arctic Ocean, including the Barents Sea (Stepanjants & Kosobokova, 2006). Type locality: central Arctic Ocean.

REMARKS: The first description of this species – as *Pararhysomedusa reesi* Shirley & Leung, 1970 – was in a photocopied and rather inaccessible publication. Stepanjants & Kosobokova (2006) put forward arguments that this publication meets the requirements of the Code of Zoological Nomenclature and that the name is available, although some doubts remain in my opinion.

Genus ***Oonautes*** Damas, 1936

Oonautes Damas, 1936; type species *Oonautes hanseni* Damas, 1936 by monotypy.

DIAGNOSIS: Medusa with eight adradial nematocyst tracks on exumbrella; broad apical chamber; manubrium very thick, with three separated rings of short tentacles, the two most oral ones somewhat larger; no marginal tentacles.

Oonautes hanseni Damas, 1936 Fig. 87

Oonautes hanseni Damas, 1936: 43, figs 1-2. – Kramp, 1959: 95, fig. 54. – Kramp, 1961: 53.

DESCRIPTION: Umbrella egg-shaped, exumbrella with eight adradial tracks of nematocysts, near the apex tracks joined pairwise in the perradii; umbrella lacking marginal tentacles, bell-margin thickened and studded with nematocysts, no ocelli. Manubrium very large and swollen, protruding out of umbrella, narrowed at the velar level, oral portion widened outside the umbrella-opening like a proboscis with two whorls of short, solid, conical tentacles; oral whorl comprises 14 very short tentacles, at some distance to oral whorl a suboral whorl with ten slightly longer tentacles; a third whorl of nine minute, tentacle-like protrusions around the middle portion of the manubrium, these gastric tentacles with rounded ends; base of stomach formed by a block of large, vacuolated cells, within the block closed cavities, four perradial channels communicate with the overlying basilar chamber above stomach; gonads absent. Four broad radial canals and a ring canal, ring canal forming apically a broad apical chamber which is connected to basilar chamber by a small opening. Colour: intense red.

DIMENSIONS: Umbrella 3 mm high.

DISTRIBUTION: Known from type locality only, off Morocco, 34.067°N 09.50°E, 0-300 m depth.

REMARKS: *Oonautes hansenii*, a species known only from a single finding, is most unusual. It is so drastically different from all other hydromedusae that one is tempted to consider it being based on an unnatural combination, e. g. of a tubulariid hydranth tucked into a degenerated *Ectopleura* medusa. Ranson (1936b), however, explicitly stated that the presumable manubrium was originally connected to the umbrella and that the separation of the manubrium and the bell (indicated by stars in Fig. 87B) happened during the sectioning process The similarity of the manubrium with hydranths of the Tubulariidae or Corymophidae remains nevertheless intriguing. A re-evaluation of the type material, especially also of its nematocyst types, is needed. Unfortunately, the type material could not be obtained.

Genus ***Tetraralphia*** Pagès & Bouillon, 1997

Tetraralphia Pagès & Bouillon, 1997, type species *Tetraralphia hypothetica* Pagès & Bouillon, 1997 by monotypy.

DIAGNOSIS (emended after Pagès & Bouillon, 1997): Medusa with scattered nematocysts on exumbrella, top of subumbrella with four interradial pockets projecting into mesogloea; four stiff marginal tentacles, each with a single, terminal, disc-shaped nematocyst cluster, four marginal bulbs with triangular nematocyst pads clasping bell margin; manubrium quadrangular to cross-shaped in section, simple circular mouth. Cnidome includes stenoteles and isorhizas.

REMARKS: See under *Tetraralphia hypothetica*.

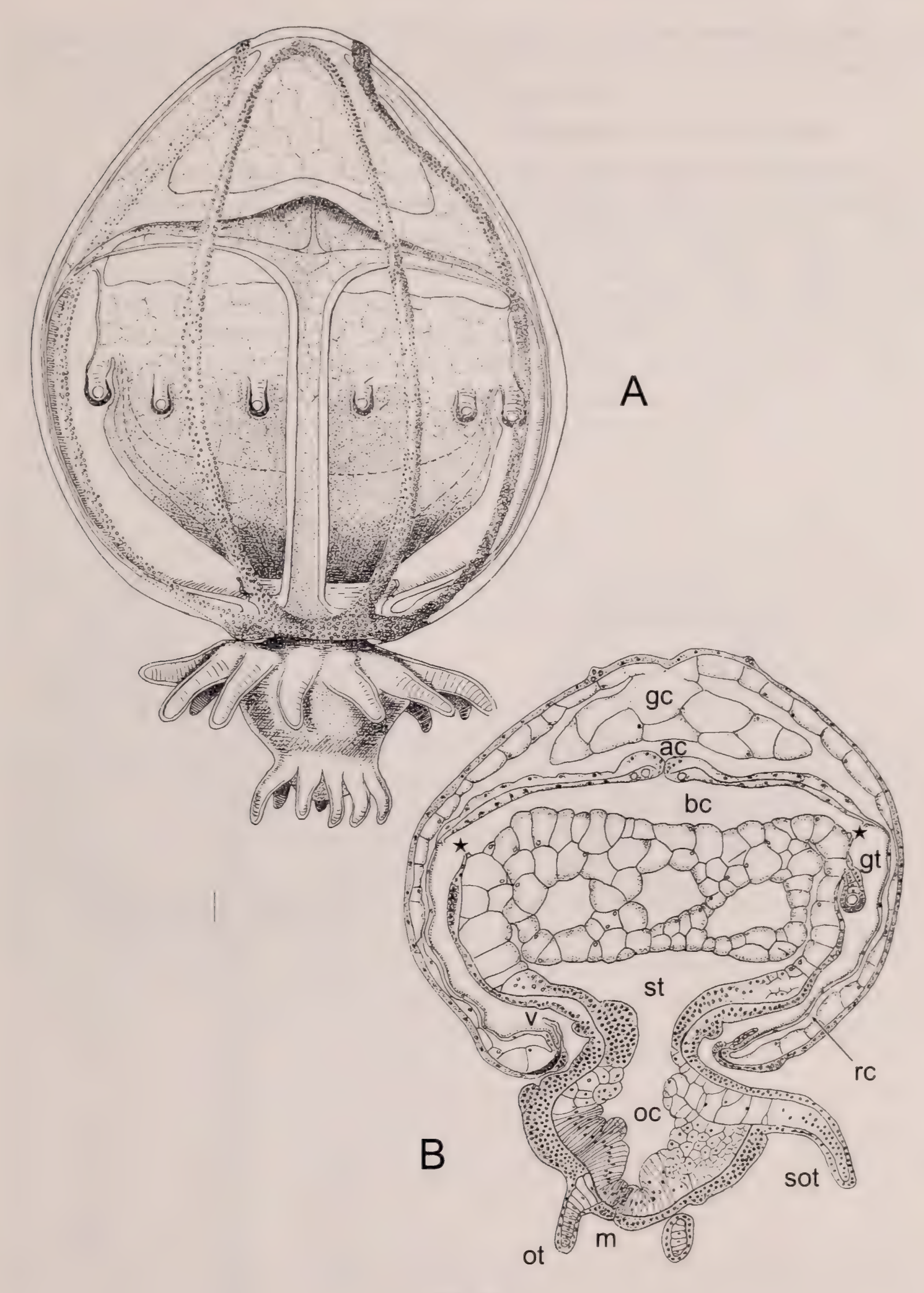


FIG. 87

Oonautes hanseni Damas, 1936; from Damas (1936). (A) Preserved animal, size 3 mm. (B) Longitudinal histological section; the two stars indicate a rupture that occurred during the sectioning. Abbreviations: *ac* apical chamber, *bc* basilar chamber, *gc* gastrodermal cushion, *gt* gastric tentacles, *m* mouth, *oc* oral cavity, *ot* oral tentacles, *rc* radial canal, *sot* suboral tentacles, *st* stomach, *v* velum.

Tetraralphia hypothetica Pagès & Bouillon, 1997 Fig. 88

Paragotoea bathybia. – Ralph, 1959: 171, fig. 1A-D. [not *Paragotoea bathybia* Kramp, 1942]
Tetraralphia hypothetica Pagès & Bouillon, 1997: 492, Fig. 1B.

Diagnosis: See genus diagnosis.

Description (after Ralph, 1959): Medusa with bell-shaped umbrella, slightly wider than high, jelly moderately thick, somewhat thicker at apex, without apical projection, gastric peduncle may be present. Manubrium large, ovoid, quadrangular to cross-shaped in section, simple circular mouth; gonad encircles manubrium, without perradial interruption. Four radial canals, issuing from top of manubrium, no mesenteries; ring canal present. Radial canals end in marginal bulbs, these mostly composed of large, triangular epidermal pad with numerous nematocysts. When fully grown with four stiff tentacles, about as long as bell height, terminating in a single, disc-shaped nematocyst cluster. Younger animals with only one or two tentacles.

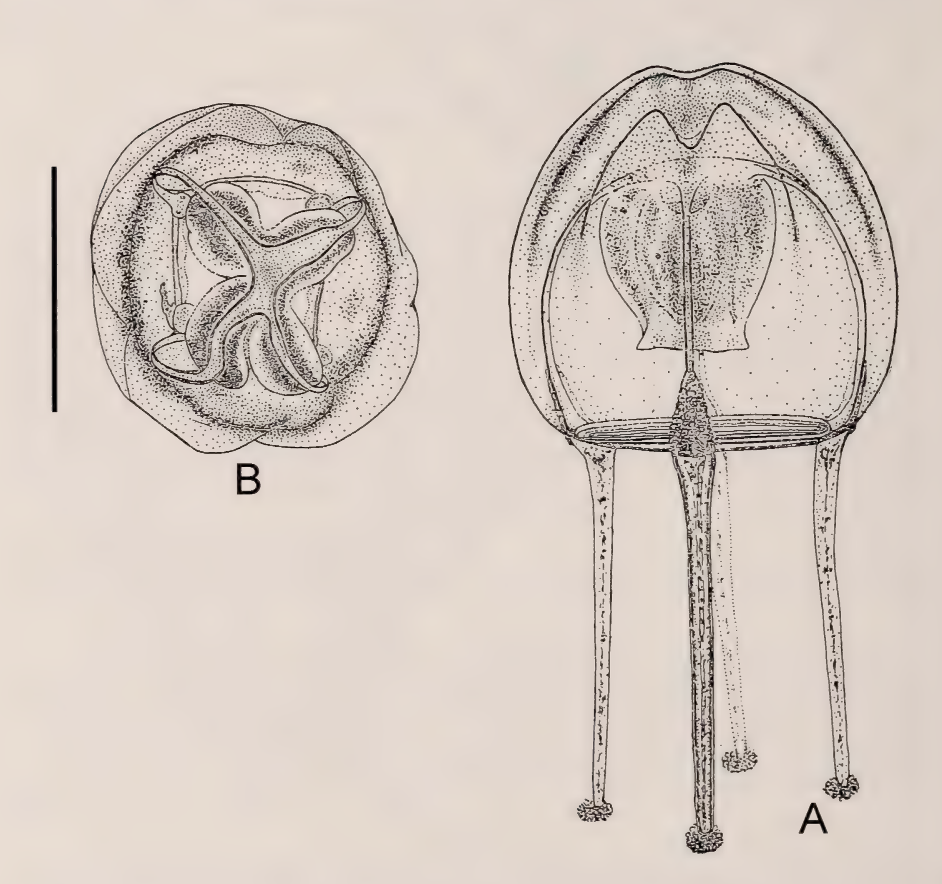


Fig. 88

Tetraralphia hypothetica Pagès & Bouillon, 1997; modified after Ralph (1959). (A) Lateral view of reconstructed medusa. (B) Aboral view of the largest observed specimen; scale bar 2 mm.

Colours: marginal nematocyst pads bright yellow-orange, top of manubrium similar but paler, rest translucent.

Nematocysts: stenoteles and atrichous isorhizas,

DIMENSIONS: Bell height up to 3.85 mm, diameter up to 4 mm.

DISTRIBUTION: Known from type locality only, deep waters of the Bay of Biscay.

REMARKS: Ralph (1959) described three mutilated medusae from the Bay of Biscay which she identified as *Paragotea bathybia*. Pagès & Bouillon (1997) obtained more samples of *P. bathybia* and realized that Ralph's medusae do not belong to this species, notably because they had more than one tentacle and subumbrellar pockets. They attributed Ralph's medusae to a new genus and species with the name *Tetraralphia hypothetica*. The largest of Ralph's three medusae originally had four tentacles, but only their basal stumps were present. The two other medusae had one and two tentacles respectively. Ralph concluded that they were part of a developmental series and that in this species the number of tentacles increases with age. Her illustration of an intact animal (Fig. 88A) is thus a somewhat hypothetical reconstruction and it is possible that Ralph's material actually comprised more than one species. This is reflected in the name *hypothetica* given by Pagès & Bouillon (1997). Ralph's material has reportedly been lost (Pagè s & Bouillon, 1997) and therefore new material of this medusa is needed to confirm the description given above and also to evaluate its taxonomic position.

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